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A TAXONOMIC SPECTRUM OF THE SECTION EU-CALLITRICHE IN THE NETHERLANDS

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INTRODUCTION

Several years ago I received the request from Dr W. H. Wachter to work up the family of the Callitrichaceae for the Flora Neerlandica.

It soon proved that doing so for this family of somewhat shady reputation in botanical circles could not be based on herbarium and literature studies only.

As for the literature: it is not very extensive and comprises only foreign works; investigations about the Dutch Callitriches are entirely missing.

Of the foreign works we mention the monographs of Kützing, Lebel, and Hegelmaier, based on morphological studies, the articles of Jörgensen and Sokolovskaja, who started cytological research, furthermore the studies of modifications by Glück, and the work of Samuelsson, in which, among other things, some geographical and ecological data are discussed.

On account of the confusion in the nomenclature—cause of which is a.o. the synonymy of Linnaeus—it is impossible, in certain cases, to determine for which species a certain investigation was made.

In the herbaria as well we find this confusion reflected, whilst moreover an insufficient knowledge of the polymorphy has given rise to many incorrect determinations.

For illustrative purposes one single example. Many people call every Callitriche with spathulate leaves *C. stagnalis*, every Callitriche with linear leaves *C. autumnalis* or *C. hamulata*, every small landform *C. palustris*. To continue, many authors consider *C. platycarpa*-plants as *C. palustris* (Hegelmaier) or determine *C. stagnalis*-plants as *C. platycarpa*, *C. truncata* as *C. autumnalis* (Lebel). Others consider every modification as a new variety at the very least.

In a situation so confused only a combination of various research methods can procure some light, and lead to a justified nomenclature. Therefore it would undoubtedly have been desirable to commence a research after e.g. the manner of the Silene-investigations by MARSDEN-JONES and TURRILL, in which next to herbarium- and literature-studies attention is paid to geography, ecology, hybridization, anatomy, cytology and modifications.

When being put into practice, such an experimental taxonomic investigation encounters difficulties however. It is a very lengthy affair and in reality only fit for teamwork. Moreover in studying the Callitrichaceae difficulties arise, which do not, or hardly, occur in the case of terrestrial plants.

We here mention a.o. the following subjects:

1) The cultivation. This makes special demands on the control of environmental conditions and is rather complicated. It is owing to special circumstances at the botanical garden "de Wolf"—we, in this instance, think of e.g. the presence of running water—that here at long last all species could be grown marvellously, in various modifications.
2) The gathering of the seeds. The plants often suffer too much if one regularly pulls up the rather fragile stems from the water to take away the ripe seeds. This is the only way in which one can have at one's disposal a sufficient quantity of seeds: having the use of extensive field-cultures where parts may be sacrificed to the harvesting of seed.
3) The raising of seedlings. This can practically only be done in field cultures under special conditions. It was only in 1953 that this could be started in the botanical garden "de Wolf".
4) Hybridization. The difference in pollination and reproduction is the reason that hybridizations can only be made in 3 out of the 5 species treated here. The structure of the very tiny flowers and their position in the axils of the leaves make it extremely difficult not to damage the rosette in case of castration. Besides, this action must be repeated about 5 times a day to flourishing stems.
5) The study of meiosis. The ♂ flowers each consist only of 1 stamen and their number on one stem is small. Moreover the stems will not tolerate a regular investigation as to the presence of anthers, they break or become too dry. So one can use each stem only once and it requires very much material before one has gathered a number of good stages.

On account of the above mentioned facts the working-program necessarily had to be curtailed.

The investigation now comprises the 5 Dutch species of the section Eu-callitriche, viz. *C. hamulata*, *C. obtusangula*, *C. stagnalis*, *C. platycarpa* and *C. palustris*. The following subjects arise:

In Ch. I a description is given of the cultures indoors and in the field.

Ch. II treats of cytology and especially mitosis. The great differences in chromosome sets proved a fit basis for the limiting of the species. In *C. palustris*, apogamous as landform, meiosis was studied and a start was made with the cytology of the ovule.

In Ch. III the most striking modifications are described.

Ch. IV gives a description of the pollination of the various species.

Ch. V gives a survey of the geographical distribution of the species in the Netherlands and in Europe and gives data about pH, salinity, vegetation etc. of various Dutch Callitriche-localities.

In connection with the sometimes striking distribution areas the germination of the seeds in solutions of various salt concentrations was studied (Ch. VI).

The nomenclature is discussed in Ch. VII, and in Ch. VIII a description is given of each species, after which there follows a key to the species.

As to *Callitriche hermaphroditica*—probably the only Dutch representative of the section Pseudo-callitriche—only herbarium material could be studied. The data about this species will be published elsewhere (Acta Botanica Neerlandica, in preparation).

ACKNOWLEDGEMENTS

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Finally I must record a special debt to Mr. E. Laarman for his interest and valuable help and to the gardeners, Mr. Medendorp, Mr. Blom, Mr. Lindeman, Mr. Lok, Mr. Robertus, Mr. Visser Sr and Mr. Visser Jr for their help in the field cultures.

LIST OF ABBREVIATIONS

Herbarium	Amsterdam	h.AMD
,,	Barbey-Boissier, Genève	h.B-B.

Herbarium	Clason (Groningen)	h.Clas.
,,	Copenhague	h.C.
,,	Delessert, Genève	h.D.
,,	Groningen	h.GRO
,,	Kern & Reichgelt (Nijmegen)	h.K. & R.
,,	Leiden	h.L. (NBV incl.)
,,	Lousley (London)	h.Ly.
,,	Schotsman (Groningen)	h.Sch.
,,	Zürich	h.Z.
living plants		x
vice county		v.c.

Chapter I

CULTURES

In the literature on this subject we find but spare data about the cultivating of Callitriche.

Askenasy (1872), Clarke (1859) and Jörgensen (1925) cultivated the plants in moist mud in flowerpots and in that manner also transferred waterforms into landforms. The plants remained alive but flowered only little and hardly set any fruit. Watercultures in glass jars gave many difficulties on account of abundant growth of algae. A rather dark place, to repress this growth, did not prove to promote the wellbeing of the Callitriches, so that none of those methods led to a useful result.

Perhaps Kirchner, Loew and Schröter (1932) experienced the same disappointments. They entirely agree with Jörgensen's information, that the Callitriches scarcely flower in cultures and hardly set any fruit.

Glück (1924) had slightly more success. He, anyway, succeeded in transferring landforms into waterforms in an unheated hothouse and to get *C. hamulata* to flower and fructification. Besides, he kept *C. obtusangula*, originating from Cambridge, alive from Oct. 1911 - June 1912. This plant developed good rosettes in the spring of 1912 and also flowered.

From the facts mentioned, it however becomes apparent that the cultures can never comprise a sufficient number of plants and that they survive only a few months.

As it is necessary for the study of lifecycles, modifications, cytological peculiarities etc. to have at one's disposal numerous plants, an investigation into fitting circumstances of cultures proved desirable in the first place.

I. Indoor Cultures

A. Waterforms. These cultures were started in Oct. 1948. In the beginning experiments were only made with *C. hamulata* (from Haren, prov. of Groningen), *C. platycarpa* (Haren, prov. of Groningen), and *C. obtusangula* (from the island of Texel). The plants were cultivated in glass jars and placed in an unheated room. As culture medium there were used: tapwater, rainwater and deep-wellwater from the pond of the botanical garden "de Wolf" with and without soilmaterial. This soil consisted of sieved leafmould or boulderclay and was added unsterilized or sterilized. This addition of soil proved neither a success in sterilized nor in unsterilized form. In nearly all cases there occurred waterpollution after a few weeks with strong growth of Cyanophyceae and Proderma viridis, so that the Callitriches expired. Tapwater too was found to be unfit. The best result, ultimately, came from rainwater. In this medium *C. platycarpa* and especially *C. hamulata* grew well, without annoying development of algae, and formed a good number of roots.

In the spring the temperature became too high in the workroom of the laboratory on sunny days, which caused a speedily turning yellow and withering of the plants. So the cultures were transferred to a part of the barn of a farmhouse, belonging to the botanical garden. These cool rooms, situated N.W. proved very favourable for the cultures. Not only rainwater cultures of *C. hamulata*, *C. platycarpa* and *C. stagnalis* succeeded well here, but also the germination of the seeds, the cultivating of the landforms and experiments regarding the salt tolerance in various species gave a good result. Moreover *C. obtusangula* was kept alive in diluted sea-water during several months, while normal flowering and fructification occurred. To prevent frostdamage to the glass jars, a fire was lit to keep the temperature just above 0° C during frostperiods.

B. Landforms. Those may easily be grown in open petridishes and be brought to flower; they were placed in the same room. As substrate, the soilsubstance of the findspot was used as much as possible. For *C. hamulata* and *C. platycarpa* this was mostly dried ditchmud, for *C. palustris* and *C. stagnalis* loamy brooksoil. The substrate was regularly kept moist with rainwater.

II. FIELDCULTURES

1) *Valley of the experimental brook*

A. Waterforms. Though the cultures progressed well indoors, several drawbacks nevertheless proved to be connected. In the first place it was not possible to grow *C. platycarpa* from the quickly flowing brooks of Limburg in this manner. Also *C. palustris* as a waterform brought difficulties. Further in several species—probably because temperature and light ratio are quite different indoors from those in the field—a diverging habit occurred and other forms of leaves. *C. hamulata* e.g. lives for years in cultures, whereas this species is a winter annual in our country. If certain observations are solely made from indoor cultures, then one soon draws conclusions that do not tally with the behaviour of the plants in the field.

To abolish the drawbacks mentioned, possibilities were sought to grow the different species in the open air, under circumstances as much as possible similar to those of the natural place of growth. This could only be realized after the watersupply of the botanical garden "de Wolf" was greatly improved in 1949. In that year a pump was set, bringing up water from a well, ± 70 m. deep, and propelling it into the brook through the arboretum and fields. In this way the water level remains up to the mark during the summer in the shallow places and moreover, in several slanting places in the brook, a fair current is caused. Because of the continuous supply of cool wellwater the temperature does not rise above 17° C in the unshaded parts; in the arboretum it is usually 15° C in summer. The growth of algae is especially inconsiderable in the arboretum, so that the botanical garden brook,—in the shady part as well as in the field part—forms an extremely fitting environment for the various species of Callitriche. The soil principally consists of sandy soils with a subsoil of boulder-clay. In the quiet parts *C. platycarpa*, *C. stagnalis*, *C. hamulata* have been grown for some years, while in the quickly flowing parts the Limburg brookform of *C. platycarpa* comes to abundant development. *C. obtusangula*, which originally would not keep for more than a few months, neither indoors, nor in the field, proved to have at last found a good place in a part of the brook covered by a thick layer of ashes. Since its having been planted in the autumn of 1951 it spreads into thick placcards of a few metres, flowers and fructificates and during the mild winters remains in good condition as well.

B. Landforms. Along the banks of the brook landforms of *C. platycarpa* and *C. hamulata* are being cultivated. Moreover *C. platycarpa* forms a vegetation continuously becoming more dense along a moist shady path between *Juncus bufonius* and a few Gramineae.

2) *"Cowpuddle" cultures*

In the marshy grasslands along the brooks of Drenthe we in summer find a bumpy piece of land, with more or less deep little hollows and cavities, caused by the cows grazing there and continually sinking their legs into the marshy soil. Henceforward these hollows will be called "cowpuddles". In these "cowpuddles", in which there is generally some water, we find a typical vegetation, consisting a.o. of land—and sometimes small waterforms of *C. stagnalis* and *C. palustris* (cf. for further peculiarities of this vegetation Ch. V).

As it was no success originally to cultivate *C. palustris* especially as a waterform, in an entirely satisfying way, the natural environment of these plants was imitated in a swampy strip of land looking suitable, along the brook, through the meadows in the botanical garden "de Wolf". At distance of a few dm. small hollows were dug of about 15 cm. diameter and about 20 cm. deep. During the winter the hollows are all full of water, in summer there is a possibility of letting some run dry. The environing vegetation (principally Gramineae and *Lotus uliginosus*) shields the plants from too strong a radiation of the sun. *C. palustris* and also *C. stagnalis*, when sown, grow into sturdy land- and waterforms. How exactly this area complies with the demands that *C. palustris* makes on its environment, appears from the spontaneous growth of scores of fructificating *C. palustris*-plants during the summer of 1953.

Also for the cultivation of seedlings the "cowpuddles" proved very efficient. In indoor cultures the seedlings rarely grow any higher than a few cm., while in the brook they usually are washed away. By means of the regulable waterlevel the transition from land- to waterform, and the other way round, can easily be studied in the "cowpuddles" without the tiresome transplanting.

Chapter II

KARYOLOGY

I. Literature

Only two authors studied karyology in some species of the section Eu-callitriche, namely Jörgensen and Sokolovskaja.

Jörgensen (1925) investigated meiosis in Danish plants and mentions a.o.: *C. hamulata*, *C. stagnalis* and *C. verna* (nomencl. Jörgensen). In the former species he found $n = 19$, in *C. stagnalis* $n = 5$ and $n = 10$, in *C. verna* $n = 10$. Moreover he studied various stages of the development of the ovules in these species. This investigation is most exhaustive in *C. autumnalis* (nomencl. Jörgensen, syn. *C. hermaphroditica* Juslen.), a species of the section Pseudo-callitriche. Probably the development in both species is rather analogous. According to Jörgensen the ovule of *C. autumnalis* shows a linear tetrad of which the chalazal megaspore forms the eight-nucleate embryosac. Also in *C. verna* he observed an eight-nucleate embryosac. In *C. autumnalis* he found after fecondation a cellular endosperm with a micropylar haustorium and a chalazal haustorium. The germ possesses a suspensor and lies in the central part of the endosperm.

In Jörgensen's article good descriptions of the species are lacking. Consequently one can not trace with certainty which species he studied. Therefore it is impossible to decide whether his *C. stagnalis* includes *C. platycarpa* or not. Also the limitation of his *C. verna* is uncertain.

Sokolovskaja (1932) has examined Russian plants. She counted the number of chromosomes in the roottips of *C. verna* (nomencl. Sokolovskaja) and *C. stagnalis* and gave a chromosome picture of both species with a table of the size of the chromosomes. She found in *C. verna* $2n = 20$ and in *C. stagnalis* $2n = 10$. Of both species—especially of *C. verna*—Sokolovskaja mentioned some clear characters. It is almost certain that her *C. verna* is morphologically identical with our *C. palustris*.

II. Material and Methods

For studying mitosis in *C. hamulata*, *C. obtusangula*, *C. platycarpa*, *C. stagnalis* and *C. palustris* Feulgen squashes of young roottips were made. The roots must be taken from waterforms; staining of landform-roots proved to be generally impossible.

Especially in *C. palustris*, mostly occurring as a landform, this fact gave rise to many difficulties. The small plants have scanty and very thin roots with a few divisions only. In the summer of 1953 however, we succeeded in obtaining well-stained clear preparations of *C. palustris*. The roots were coming from waterforms of an inundated brookvalley and from cultures in the botanical garden "de Wolf".

As to *C. hamulata* the roots were generally gathered in autumn, a period of intense vegetative growth. For *C. obtusangula*, *C. platycarpa* and *C. stagnalis* spring and early summer proved the most successful time.

The procedure adopted for making the Feulgen squashes was as follows:

1) Pre-treatment in 0.129 mol. α-8-hydroxychinoline solution for 2-4 hours.
2) Fix in Carnoy for ¾ hours.
3) Transfer to 100 % alcohol for 12 to 24 hours.
4) Hydrolyse in 0.1 *n* HCl at 60° C for 8 to 10 minutes.
5) Stain by Feulgen (basic fuchsin).
6) Transfer to water for 30 minutes.
7) Transfer to 45 % acetic acid on a slide, cover, tease out and squash.

The procedure for making preparations permanent was as follows:

1) Dissolve the cover slip by immersing the preparation in Carnoy.
2) Pass through absolute alcohol.
3) Mount in "euparal".

Meiosis and the development of the ovule were studied in *C. palustris*. As this species is rare in the Netherlands, we had only the disposal of a small number of anthers and ovules. Most of the material came from our own cultures in the botanical garden "de Wolf".

The anthers and ovules were fixed in Randolph's modification of Navashin, embedded in paraffin, sectioned 7 μ and stained with crystal violet.

The chromosome pictures were drawn after metaphase-chromosomes with the aid of a drawing-prism. In various metaphaseplates of one roottip the length of corresponding chromosomes may be different, so there can not be attached absolute value to the length of the chromosomes in a chromosome picture. A picture gives an impression only of the relative ratio of length of the chromosomes in one set and of the place of the centromeres.

For a good comparison of the sets of the various species it is necessary to choose the possibly most corresponding stages. Nevertheless exact comparison is out of the question.

III. OBSERVATIONS

A. Mitosis

1. **C. hamulata** (h.Sch. 51104, 52147, 5340)

The number of chromosomes is $2n = 38$ (plate 1). This number is quite in agreement with the statement of JÖRGENSEN (1925). We found that the chromosomes normally—without cold treatment—are heterochromatic. The other species show this phenomenon as well, especially it is very clear in *C. stagnalis* (plate 2*b*).

The chromosomes are of different length and possess median, submedian or subterminal centromeres. The latter type is the most frequent (17 pairs). In a few chromosomes the short arm is very small. There is only one pair of long chromosomes with a median centromere, and one pair with submedian (fig. 1*e*). Generally the former chromosomes are V-shaped, sometimes the arms are in prolongation of one another (plate 2*e*).

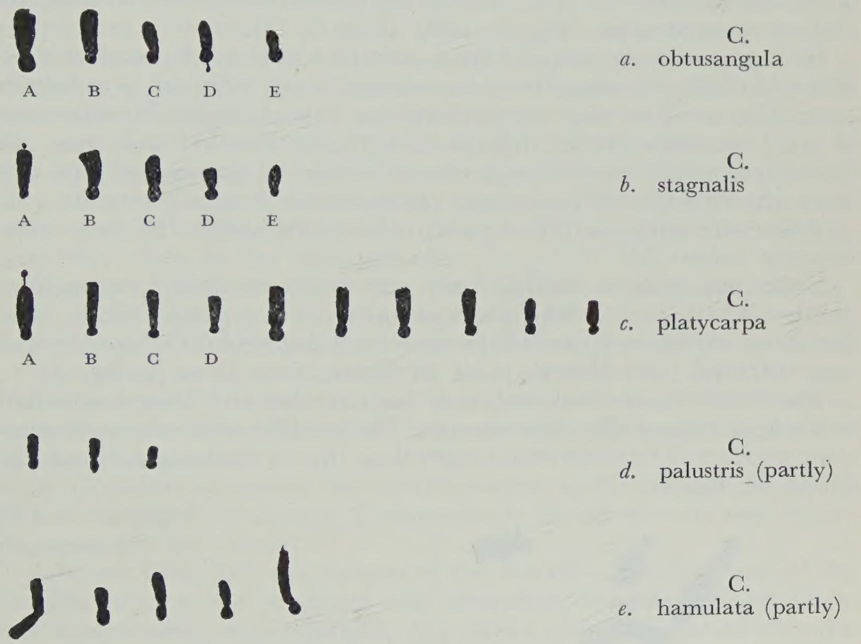


Fig. 1. Chromosome pictures. × 2400.

In the section Eu-callitriche *C. hamulata* is the only European species possessing chromosomes with median centromeres.

2. **C. obtusangula** (plants from the Isle of Texel: h.Sch. 51292, 51293; plants from the prov. of Zeeland: h.Sch. 5301)

This species has $2n = 10$ (plate 3*d*). In the haploid set one long chromosome can be observed, possessing a subterminal centromere (fig. 1*a*, chr. A). Chromosome B (fig. 1*a*) is somewhat smaller and shows a subterminal centromere as well. The short arm of this chromosome is very small. Moreover there are two medium-sized chromosomes with subterminal centromeres (fig. 1*a*, chr. C, D) and one small chromosome with a submedian constriction (fig. 1*a*, chr. E). All chromosomes are heterochromatic.

It is a striking fact that in this species we meet with plants having

0 or 2 SAT-chromosomes. The former type occurs in the island of Texel, whereas plants with 2 SAT-chromosomes are to be found in the province of Zeeland (plate 3*e*).

The satellites are small, nearly globular and connected with the short arms of one pair of medium-sized chromosomes (fig. 1*a*, chr. D). For more details concerning the structure of the satellite cf. *C. stagnalis.*

3. **C. platycarpa** (h.Sch. 5130, 5133, 5140, 52130)

This species has $2n = 20$ (plate 2*a*). The chromosomes are heterochromatic and all of them possess a subterminal centromere (fig. 1*c*). They are of different size. 4 Pairs of chromosomes are striking by their very small arms (fig. 1*c*, chr. A, B, C, D).

In *C. platycarpa* we found plants with 0, 1 or 2 SAT-chromosomes. When 2 SAT-chromosomes are present, two different possibilities arise. The satellites may occur either on 2 homologous chromosomes or on 2 chromosomes of different length. In the first case they are connected with a pair of long chromosomes, in the second case one short chromosome and one long chromosome possess a satellite.

When only one satellite is present, it is attached to the long chromosome (plate 2*d*).

Sometimes in one locality only one type was found, sometimes plants with 0, 1 or 2 SAT-chromosomes occur together. Only once the above mentioned case of two non-homologous SAT-chromosomes was observed (viz. Haren, prov. of Groningen; plate 2*c*, fig. 2).

The satellites are small, more or less globular and always attached to the long arms of the chromosomes. The satellite of the short chromosome appears to be somewhat longer than that of the long chromosome (plate 2*c*, fig. 2).

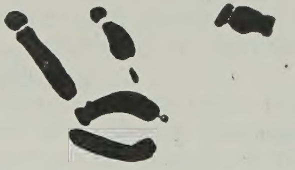


Fig. 2. Explanatory diagram of the left part of plate 2c.

4. **C. stagnalis** (h.Sch. 51109)

The number of chromosomes is $2n = 10$ (plate 3*a*). All chromosomes have a subterminal centromere; they are heterochromatic (plate 2*b*). Three pairs of long chromosomes show about the same length. The first pair (fig. 1*b*, chr. A) is clearly distinguishable from the others by the very small short arm, the second and third pair mutually are nearly analogous (fig. 1*b*, chr. B and C). The fourth and fifth pair are much smaller, resembling each other in total length, but there is a clear difference in the position of the centromere (fig. 1*b*, chr. D and E).

In this species we meet with plants having 0, 1 or 2 SAT-chromosomes (plate 3*a*, *b*, *c*). No morphological differences between the plants could be observed. In some localities only one type was found (a.o. in Middachten, prov. of Gelderland, 2 SAT-chrom.); in Schipborg (prov. of Drenthe), however, the three types occur together.

Only the pair of long chromosomes with the most terminally placed centromere possesses the satellites (fig. 1*b*, chr. A).

It should be emphasized, that in the case of only one SAT-chromosome being present, the homologous chromosome does not possess a satellite.

The satellite is small, nearly globular and attached to the long arm of the chromosome. It has been proved that each satellite in the prophase consists of 2 markedly defined parts, connected with each other by a threadlike connection (plate 4*a*, *b*). In the centre of this connection ("thread") a small thickening is visible (plate 4*c*, *d*). In this stage the satellite has removed from its chromosome over a distance as long as the chromosome itself, and an extremely thin connective "thread" is seen between the one part of the satellite and the end of the chromosome (plate 4*a-d*). Later on the two parts of the satellite approach each other more and more (plate 4*e*, *f*) until they form a whole. The threadlike connection between the chromosome and its satellite shortens so that in the metaphase the satellite gets very close to the chromosome.

Gosselin (1946) observed that the satellites of *Anthurium*, *Xanthosoma*, *Washingtonia*, and *Hedychium* in the prophase consist of two parts as well, one of them being connected with the end of the chromosome.

According to Gosselin however this latter part, called by him "chromocentre", disappears into the chromosome as "un bouchon dans le goulot d'une bouteille", whereas the other part remains out of the chromosome.

So Gosselin considered the satellite visible in the metaphase as one of the two parts mentioned. Unfortunately his pictures do not clearly demonstrate his theory.

Anyhow Gosselin's description of the behaviour of the parts of the satellites during the prophase and metaphase is quite different from our observations in Callitriche. We never observed one of the two parts disappearing into the chromosomes. Always both parts approach each other until they have united and as a result of proceeding contraction the satellite as a whole is coming close to the chromosome.

In *C. obtusangula* this phenomenon could be observed as well. Up till now we did not meet with *C. stagnalis*-plants with $2n = 20$, such as Jörgensen mentions. It may be possible that this number has reference to *C. platycarpa*, with which *C. stagnalis* often has been confused. In the absence of a good description of Jörgensen's material, this cannot be decided.

The chromosome set as we found this in Dutch plants is different from the set, pictured by Sokolovskaja (cf. fig. 1*b* with fig. 3). The small chromosomes D and E—very striking in our plants—are lacking in the picture given by Sokolovskaja. Her figure shows only one somewhat smaller chromosome, nearly as long as the others (chr. I). In the Dutch material, however, the 2 small chromosomes are about half as long as the other ones.

Besides Sokolovskaja found 2 chromosomes with a very short arm, being nearly similar in size (chr. IV, V). We too, found 2 chromosomes with a very short arm, however greatly differing in size; one belongs to the long chromosomes, the other to the short ones (fig. 1*b*, chr. A and E).

Sokolovskaja did not pre-treat her material, so it is not quite comparable with ours. We, however, compared the sets of untreated and pre-treated roots in *C. obtusangula* with each other. From this it may be concluded that the mutual ratio of length of the chromosomes does not change by the treatment, while the chromosomes contract proportionally. Also in the chromosome picture given by Sokolovskaja we should expect the two small chromosomes D and E to attract our attention, while the two chromosomes with a short arm should markedly differ in length. This, however, is not so. The difference in picture could possibly be explained on the assumption that Sokolovskaja found great difficulty in observing the chromosome lenghts in her material being untreated. For only rarely a chromosome in the equatorial plate is uncoiled and in its entirety visible. Pre-treated material certainly provides a more reliable result in determining the mutual ratio of length. It may, however, be possible that the Russian specimens possess a chromosome set different from that of our Dutch plants.

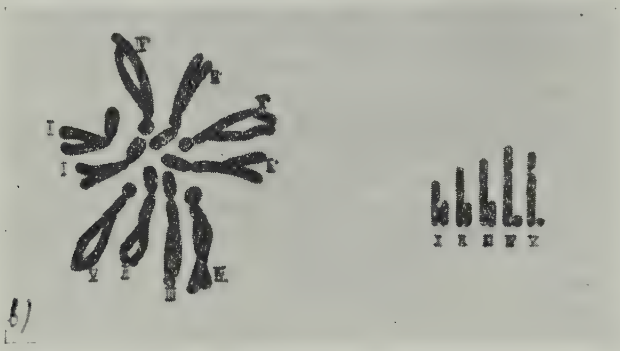


Fig. 3. C. stagnalis. After Sokolovskaja (1928). For explanation see text.

5. **C. palustris** (h.Sch. 5349)

The number of chromosomes is $2n = 20$ (plate 3*f*). They are all heterochromatic and have a subterminal centromere. As to the smallest pair we might speak of a submedian centromere, but because of the very small size it is difficult to decide between the two types.

The chromosome set pictured by Sokolovskaja, is different from the set we found (cf. fig. 4). Several chromosomes of Sokolovskaja's *C. verna* (= our *C. palustris*) are of the same size as the longest in *C. stagnalis*, but according to our observations the longest chromosomes of *C. palustris* are only somewhat larger than the smallest ones of *C. stagnalis* (fig. 1*d*).

Of all species in the section Eu-callitriche *C. palustris* possesses the smallest chromosomes. In this species again we meet with plants, having 0 or 2 SAT-chromosomes (plate 3*f*, *g*).

The satellites are very small and are connected with the short arms of two homologous chromosomes.

It is a striking fact that several chromosomes in the metaphase are connected with each other by more or less broad, stained "threads" (plate 6*a*, *b*). Mostly the short arms of the chromosomes are attached to each other, but sometimes the short arm of one chromosome is joined to the long arm of another. The total number of joined chromosomes ranges from 6 to 18; they are generally divided into two or more groups. So it should be emphasized that not only homologous chromosomes are connected.

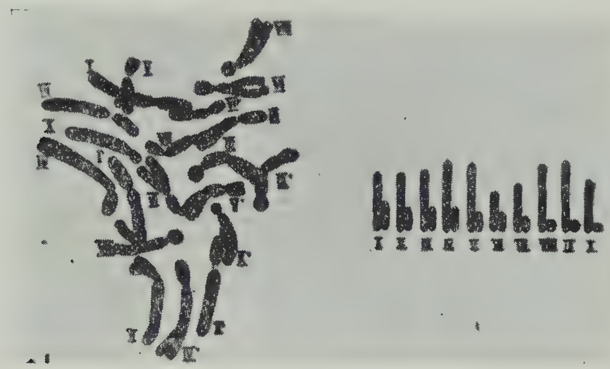


Fig. 4. C. palustris. After Sokolovskaja (1928). For explanation see text.

B. Meiosis

C. palustris (h.Sch. 5349)

In the waterforms, possessing well developed stamens, the meiotic division generally is entirely normal. Pairing is regular, ten bivalents are formed and consequently M_I and M_{II} are quite normal (plate 2*f*, *g*).

In several anthers, however, we meet with irregularities in the meiosis of the exterior PMC's; the chromosomes become more or less sticky. Hence in many ripe, apparently well developed anthers only the central pollengrains are normal in size and shape. In the landforms the stamens at best develop into a clavate body, showing in the upper part a few PMC's. In this case, however, a regular meiosis was never observed, the chromosomes being very sticky. Sometimes in older stages a few pollengrains have been seen, which are always shrunken.

C. Development of the ovule

C. palustris

The pistils of the investigated landforms all show abortive stigmata. The ovules are anatropous. The first stages in the development are quite normal. The large EMC in prophase, dyads and especially the T-shaped tetrad (different from the linear tetrad Jörgensen mentions in *C. autumnalis*) have been seen several times (plate 5*a*). The number of chromosomes in the tetrad—when it could be counted—was 10.

Various times we observed a large cell lying below or somewhat at the side of the chalazal part of the tetrad (plate 5*b*, *c*). This cell, forming part of the surrounding tissue of the nucellus, must possess 20 chromosomes. To all appearance the tetrad is crushed by the development of this cell. In further stages remains of the four cells of the tetrad could be observed, lying above the enlarged somatic cell. Because the chromosomes in the observed metaphase plates always are very close together, only 17 chromosomes could be well counted (plate 5*b*, *c*).

The first divisions of the somatic cell were not observed, but in some ovules a large embryosac was seen with again a crushed mass of cells above it.

The chalazal part of this embryosac has a granulous content, the upper part is transparent. The border-line runs nearly across the middle. In the earliest stage of development observed, a large dividing nucleus was visible on either side of the border-line. Three antipods occur on the chalazal side. On the micropylar side only one nucleus could be distinguished, so either the embryosac is six-nucleate or the one or two present synergids soon disappear.

In older ovules a normally developed cellular endosperm is present. The germ lies in the centre of the endosperm, provided with a short suspensor. The chalazal haustorium is well developed and consists of 4 elongated cells (plate 6*c*). The apical haustorium is not clearly distinguishable. In the endospermcells about 20 chromosomes were counted.

Chapter III

MODIFICATIONS

The genus Callitriche shows a great variety of forms, just like many other waterplants. This is apparent principally in the vegetative organs.

The most remarkable thing in this respect is the difference between the land- and waterforms of one and the same species, but also the waterforms of one species can appear to us in manifold shapes, because the depth of the water, the speed of the current, the change of the seasons and the lightratio are of great influence on habit and leafshape.

So far as we know Kützing was the first to assemble a wide variety of forms of growth. The country round Schleusingen near Coburg, whence he gathered his material, was apparently a varied land, where *C. hamulata*, *C. platycarpa*, *C. stagnalis* and *C. palustris* grew in innumerable modifications. From the herbarium material collected by him (coll. Rijksherbarium, Leiden) the many drawings in Reichenbach's Iconografia botanica, and from his extensive systematical arrangement of the forms it becomes clear how intensely his attention was drawn to the polymorphy of Callitriche. In his field observations he remarks a.o. that when the environment dries up, waterforms can change into plants with quite a different habit. After Kützing several authors paid attention to the variation in habit and leafshape in Callitriche, as e.g. HEGELMAIER (1864).

Further some people tried to transform different forms of growth to each other by changing the environments. CLARKE (1859), ASKENASY (1872) and later JÖRGENSEN (1925) cultivated originally submerged plants in flowerpots and in this way obtained some landforms.

GLÜCK (1924) at last, gave a good survey of the influence of the depth of the water on the shape of the leaves and the lengths of the plants, based on numerous field observations. His data on *C. hamulata*, *C. obtusangula* and *C. verna* (*C. palustris*) can nearly all be checked. He, however, also considered *C. platycarpa*-plants as *C. stagnalis*, and this confusion makes his table and description of *C. stagnalis* practically useless.

To get a better survey of the richness in shape of the various species *C. hamulata*, *C. platycarpa*, *C. obtusangula*, *C. stagnalis* and *C. palustris* were observed during some years in the botanical garden "de Wolf" under varying circumstances. Of waterforms separated parts of homogeneous placcards were planted, of landforms as many cuttings of one plant as possible were planted in the several environments. Only for *C. palustris* separate plants had to be used as those are thin and little branched.

The plants were set in almost stagnant water of various depths, in running water, in moist soil, in "cowpuddles" shaded by the surrounding vegetation and in "cowpuddles" without surrounding vegetation. By altering the waterlevel, waterforms could on the spot grow into landforms and the other way round. Moreover, the habit and the leafshape during the seasons were observed.

As *C. obtusangula* in "de Wolf" only develops properly on a layer of ashes, so on a substrate diverging from the natural one, the habit- and leafchanges of this species were, during the years of observation, continually compared to those of specimina in the island of Texel. As far as it was possible the forms of growth in the cultures were also compared to those in the corresponding spots in nature for the other species.

In the survey following below only the most characteristic modifications are described, and we must always remember that the descriptions are only valid for certain plants under certain circumstances. We may, it is true, expect a fairly general validity supported by many fieldobservations, but this does not alter the fact that these extremely variable plants can place us face to face with surprises, again and again.

1. **C. hamulata** All plants from the village of Haren (prov. of Groningen)

a) In the several seasons

The plants lived in water of 30-40 cm. deep, with but very little current. This generally winterannual species forms exclusively linear leaves after having germinated in the autumn. The plants, growing quickly and branching, remain below the surface. In spring, at the beginning of the flowering period, the rosettes, floating on the surface, composed of spathulate leaves, appear after a few elliptic leaves (plate 7*a*).

During spring and summer spathulate leaves are formed, so that by the time the plants wither, the stems, reaching as high as the waterlevel, carry mostly spathulate leaves.

b) In water of about 20, 40, and 60 cm. deep

The plants in the spots 20 cm. and 40 cm. deep form rosettes floating on the surface with spathulate leaves, during the flowering period.

In deeper water the stems generally remain submerged, with only linear leaves. Sometimes slightly broader leaves are formed, close to the surface. Wholly submerged plants also flower and fructify amply (cf. pollination Ch. IV).

c) As landform

When the hollows, in which waterforms grow, are laid dry, the greater part of the stems perish. New, prostrate or ascendent shoots appear, with small elliptic leaves. Usually the landforms fructify abundantly (cf. Ch. IV).

A remarkable phenomenon was the growth of stalked fruits in some landforms. This was observed in the fields a.o. in a vegetation near Haren (1950) and along the rim of a cattlepond in Texel (1953).

In 1953 numerous landforms grew with stalked fruits in the cultures in "de Wolf". In November 1952 young waterforms had been brought to some "cowpuddles". The depth of the water was about 15 cm. during the wintermonths. The plants were offspring of a spontaneously grown *C. hamulata*-vegetation which, for a few consecutive years, occurred in two ditches in the botanical garden. The fruits of these plants were always sessile. During spring and early summer of 1953 flowering and fructification were abundant. The fruits were sessile, as before. In June the hollows were laid dry. The original stems withered and new shoots formed a patch of flowering landforms, in which about the middle of July numerous stalked fruits could be observed. The stalks had a maximum length of about 1 cm. The fruits principally grew on the branches lying flat on the substrate. The ascending stem-parts in the dense parts of the vegetation showed mostly sessile fruits. Sometimes non-stalked and stalked fruits alternated (plate 13*a*).

It will have to be examined more closely whether the possibility of forming stalked fruits is characteristic for all *C. hamulata*-plants under certain circumstances, or whether it is a hereditary trait of some individuals.

d) In quickly running water of about 20 cm. deep

In quickly running water floating stems, sometimes more than

½ m. long, are formed with only linear leaves. Those can grow to a length of about 4 cm. Rosettes do not occur in this habitat. Flowering and fructification proceed as usual (vide Ch. IV).

e) In sun and shade, waterdepth about 30 cm., with little current
In sunny places the manner of growing of this species is approximately the same as in shady ones. The leaves of the rosettes usually become yellow in the sun however, and the plants die sooner than in the shady habitats. By continually supplying cool wellwater the difference in temperature between the two places was but small.

2. **C. obtusangula**

a) In the various seasons
Plants from the island of Texel
Plants in running and almost stagnant water of about 30 cm. deep. *C. obtusangula* is a perennial, bearing full, floating rosettes in spring and summer during the flowering period, the leaves being rhombic (plate 8*a*). About October-November linear leaves are formed at last, after pairs of narrower leaves (plate 11). The many branches, growing in this period, all show the same type of leaf too. The species hibernates in more or less dense patches of branched stems, mostly remaining entirely submerged (plate 10).

b) In water of various depths
Plants from the island of Texel
In water only a few cm. to 30 cm. deep the stems form well developed floating rosettes on the surface. As this species was hard to grow outside the layer of ashes, observations in deeper water are missing. One plant having spontaneously come up in 1952 in the test-area, in about 60 cm. deep water, reached the surface with the tops of its stems in June 1953 and formed a few small rosettes with tiny lightgreen rhombshaped leaves. The stemleaves were linear. A few flowers did appear but fructification was not observed.

c) As landform
Plants from the island of Texel
The landforms show great likeness to the waterforms. When the habitat is laid dry during the flowering period, the original stems do not perish, so that the rosettes usually remain clearly visible during some dry weeks. Growth is very tardy. New leaves in the rosettes are usually narrower than the rhombshaped ones of the waterforms, those of new shoots are narrow elliptic. The colour turns a yellowish green. *C. obtusangula* is probably, also on account of the somewhat fleshy leaf better able to stand drought than the other species. Waterforms often remained lying on the dry soil for months without showing much change. Also in very sunny habitats e.g. in dried up cattleponds in Texel they maintained themselves excellently.

Plants from the province of Zeeland
For this type the same holds good. The stems and compact rosettes

with the firm, circular, sometimes truncated leaves are well proof against desiccation.

d) In quickly running water, depth about 30 cm.
As cultivating this species in the botanical garden is possible only in the presence of a layer of ashes, and this is entirely lacking in quickly running parts of the brook, it was not possible to follow the behaviour of *C. obtusangula* sufficiently. Anyhow specimina were found in Texel during April and May in a swiftly flowing watercourse from the dunes. A rosette was not formed, the topmost leaves were narrow elliptical to narrow rhombshaped. Flowers were not found.

e) In sun and shade
Plants from the island of Texel in 20 cm. deep water with little current
No clear difference was to be observed between the two forms, the rosettes remained a fresh green.

3. **C. platycarpa**

a. In the course of the seasons

1) Plants from Haren (prov. of Groningen) and Arcen (prov. of Limburg). In 30-40 cm. deep water with very little current. During the winter one generally sees stems with linear leaves, as well in old hibernating plants as in young specimina germinated in autumn. In spring, after a few narrowly elliptical leaves floating rosettes with nearly elliptical leaves are found (plate 12).
2) In quickly flowing water of about 20 cm. deep. Plants from Haren (prov. of Groningen) and Arcen (prov. of Limburg). During the whole year elliptical leaves are seen on these plants. Sometimes young sidebranches originally bear linear leaves, but only a few pair of them.

b. In water of various depths
Plants from Haren (prov. of Groningen), Arcen (prov. of Limburg) and Winterswijk (prov. of Gelderland)
Up to a depth of 40 cm. the plants form floating rosettes on the surface (plate 7*b*). At greater depth they remain submerged. The leaves are then linear and fructification does not occur (cf. Ch. IV).

c. As landform (plate 13*b*)
Plants from Haren (prov. of Groningen)
The landform of this species sometimes is very similar in habit to that of *C. hamulata* or of *C. stagnalis*. The creeping or ascendent stems bear small, more or less broad elliptical leaves and there is no rosette. Sometimes the seeds turn a lighter shade than those of the waterform and the wings somewhat broader. On account of this fact they have a tendency to resemble the fruits and seeds of *C. stagnalis.*

d. In a swift current
Plants from Haren (prov. of Groningen) and Arcen (prov. of Limburg)

The stems become floating, quite ½ m. long, limp, with large, elliptical, somewhat flabby leaves. A floating rosette is not formed, on account of the continuous movement of the water the leaves are nearly all submerged. Sometimes a few flowers appear, but owing to the fact that no pollination can take place under water, no fructification occurs.

e. In sun and shade

Plants from Haren (prov. of Groningen). Sunny habitat about 30 cm. deep with little current. Shady habitat: "cowpuddles" with about 15 cm. of water.

The rosette leaves of the plants in the sunny habitat usually turn yellowish, rather small and a little hard. The leaves of the shadeforms are big, limp and fresh green. In the "cowpuddles" shaded by grass sometimes rosettes developed with nearly circular leaves. These plants have therefore become vegetatively greatly similar to *C. stagnalis.*

4. **C. stagnalis** Plants from Schipborg (prov. of Drenthe)

a. During the seasons

In the "cowpuddles" *C. stagnalis* usually perishes in winter. Neither in the brookvalleys of Drenthe is this plant to be found during this period. Now and then a few specimina remain alive in the "cowpuddles" of the botanical garden "de Wolf", but in running water they hibernated exceptionally well. The leaves, in summer broad elliptical to nearly circular (plate 9*a*), grow slightly narrower in winter, but linear leaves I never observed on *C. stagnalis.* Compared to the other species *C. stagnalis* remains almost constant in habit and leafshape all the year round and under all sorts of conditions, which already struck Kützing.

b. In various depths of water

This species changes but little, up to a depth of about 35 cm. In the deeper parts the plants did not remain alive long. The forming of linear leaves was never observed.

c. As landform

The leaves are smaller in size than in the case of the waterforms, but remain nearly circular.

d. In flowing water

This species is not subject to any essential change of leafshape and habit. The ♀ flowers—perhaps because they are not fertilized—present longer stigmas than the plants in quieter water. Besides, the stigmas generally do not bend down, but remain a little patulous, on account of which they begin to resemble the flowers of *C. platycarpa.*

e. In sun and shade

No distinct differences could be ascertained.

5. **C. palustris.** Plants from Schipborg (prov. of Drenthe)

a. During the seasons

Plants in "cowpuddles" with about 10 cm. of water and as landform.

This plant, a summer annual in our country, forms pairs of leaves after germination in spring, with linear leaves. When the tops of the stems reach the surface, floating rosettes with spathulated leaves are formed (plate 9*b*). Trying to make this species hibernate never met with any success. Also the landforms perished in autumn, in all cases.

b. In various depths of water

This frail, delicate plant only grows as a waterform in stagnant water of about 20 cm. depth and then forms rosette-bearing stems. The flowers are usually of normal structure in this form (cf. Ch. IV).

It proved impossible to grow *C. palustris* at greater depth. Plants with lengths of more than about 25 cm. are therefore an exception. Only once a very sturdy specimen was found in herbarium material, viz. from Maikeniemenjoki (Finl.). Its length was about 60 cm.

c. As landform

C. palustris mostly occurs as landform. The plants are very small, with tiny, narrowly elliptical or obtuse-linear leaves. Vegetatively they can resemble small landforms of *C. hamulata* and *C. platycarpa*. The flowers are greatly reduced (cf. Ch. IV).

d. In swiftly flowing water

It proved impossible to cultivate this species in the flowing current of the experimental brook. The fragile stems with their frail habit do not seem able to stand a strong movement of the water. In his investigation along the skaror-coast of Finland, Luther (1951) observed that *C. palustris* always grows in places out of reach of the wash of the waves.

The species only grows in small, shallow quantities of water (cf. Ch. V).

e. In sun and shade

No distinct differences could be observed.

Chapter IV

POLLINATION AND REPRODUCTION

Most species of the section Eu-callitriche show a normal sexual reproduction, only *C. palustris*—when a landform—is an apogamous species.

In the species, showing a normal reproduction, two different manners of pollination occur: in *C. obtusangula*, *C. platycarpa* and *C. stagnalis* pollination is aerial, in *C. hamulata* it is submerged.

1. C. obtusangula, C. platycarpa and C. stagnalis

As for the aerial pollination: already older authors, as Ruprecht and Lebel had observed this fairly accurately, so that we can be short on this subject. The stamina rise above the floating rosette. When the anthers dehisce, the yellow pollengrains are strewn over the surface of the water and remain floating there. The stigmas, emerging partly from the water, in this way easily come into contact with the pollengrains. Sometimes the pollen drops straight on to the stigmas of a neighbouring flower. No sign of entomophily, as LUDWIG (1881) suggested, was seen.

After fertilization the overblown flowers gradually submerge owing to the further development of the rosette, and so the fruits ripen under water. The pollengrains of this species are provided with a distinct exine, covered with little warts. The shape differs as to the species. In this way *C. obtusangula* has ellipsoidal pollengrains and *C. stagnalis* nearly globular ones, whilst those of *C. platycarpa* show a great variety of shape. Some are nearly globular, others rounded tetrahedral or short-ellipsoidal.

In the case of landforms we also find normal pollination and fructification.

2. **C. hamulata**

In *C. hamulata* the situation is quite different. This species does form rosettes on the surface in not too deep, quiet water, but the occurrence of well developed flowers is not restricted to the occurrence of rosettes, as in the case of *C. obtusangula*, *C. stagnalis* and *C. platycarpa*. The first flowers of *C. hamulata* appear in the axils of the lower pairs of leaves. In the leafaxils higher up we gradually find younger stages of development of the flowers.

In the rosettes as well flowers at last appear, but their position and structure is always such as to make them quite submerged.

Ruprecht and Lebel also knew of the developing of flowers under water, and had at the same time observed the always abundant fructification.

BEGER (1932) considers the occurring of submerged flowers a characteristic, specific for *C. hamulata*, and—taking into consideration the abundant fructification—he suggests submerged pollination, but the observation of this event was still lacking. And yet KÜTZING (1832) and HEGELMAIER (1867), about a hundred years ago, were very close to solving the enigma of the submerged pollination. Kützing gave an excellent—though very short—description of the flowers in Linnaea. The position of the threadlike stigmata in regard to the stamen and also the bending of the stamen towards one of the stigmata at the time of pollination, was observed by him quite accurately. Therefore it is remarkable that the position of the styles in this flower was misdrawn in Reichenbach's Iconographia botanica as well as in the Icones.

Hegelmaier also distinguished the existence of entirely submerged flowers in *C. hamulata* and even found anthers in which there occurred pollengrains with a "farblose und glatte Aussenhaut" and specimina for which he "die Anwesenheit einer Exine nicht konstatieren konnte". He imagined however that this pollen was not yet ripe and then he comes to the conclusion in 1867 that he is convinced by his observations that *C. hamulata* has yellow pollen and that the normal pollination is aerial.

Let us study the flowers of *C. hamulata* closer after these data from literature.

The nearly sessile ovary bears at the top 2 transverse threadshaped stigmata, directly reflexed at the base. They are directed obliquely backwards, so that on either side of the stem they protrude slightly under the leafaxil with the ♂ flower (plate 14*a*). The small stamen, originally visible as a green sessile little globe, possesses a quickly growing filament which soon bends towards one of the stigmata, so that the reniform unilocular anther comes to rest against that stigma (fig. 5).

Against the time that the anthers are going to dehisce, the wall is coloured light yellow. The pollination now proceeds as follows: at the top of the ripe anthers there appears a longitudinal rent and a colourless very coherent mass of pollengrains becomes visible. These pollengrains are globular and very thin-walled. Neither of an exine, nor of a walldesign anything can be seen. They are nearly full of starchgrains (blue with KJ). Not long after the grains have come into contact with the surrounding water, the pollentubes begin to develop (fig. 5). Within a few hours there appear long winding tubes, forcing their way into the stigmatic tissue. The transition from style to stigma is not quite clear in Callitriche; most probably the whole organ works as a stigma, as at the base germinating grains were observed as well.

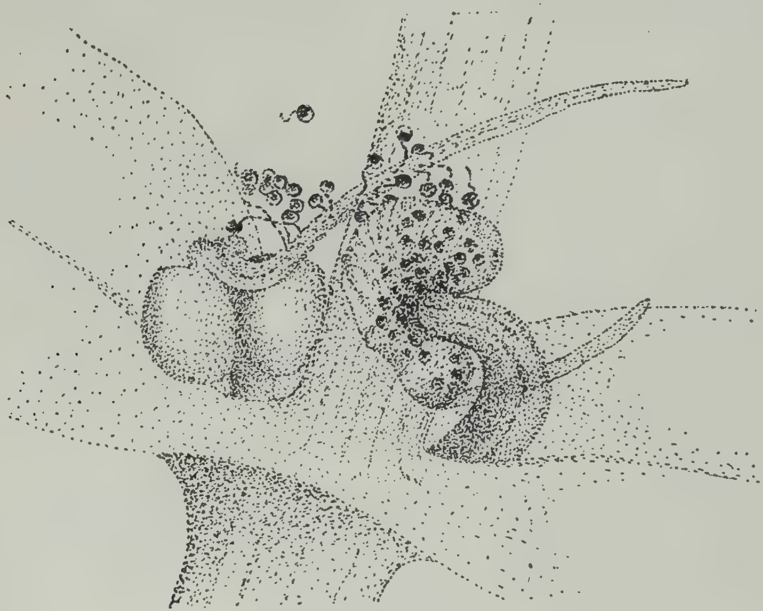


Fig. 5. C. hamulata. Submerged pollination.

Usually the mass of pollen in an anther remains very coherent, sometimes also smaller or larger ball-like groups of germinated pollengrains detach themselves and remain suspended in the water.

Landforms too usually fructify well. Often we can find little drops (usually due to dew or rain) in leafaxils, in which pollengrains have germinated.

The colourless pollen without exine also occurs in other waterplants, for which it has been stated that the pollination is submerged. In *Zannichellia* and *Najas* the grains are globular as in *C. hamulata*, in *Zostera*, *Posidonia*, *Halophila* and *Cymodocea* the pollen is confervoid (ROSE 1887, CLAVAUD 1878).

As for *Najas*, JÖNSSON (1883) mentions that the pollen is "helt full-propade med stärkelse korn", while HOFMEISTER (1852) and MAGNUS (1894) saw that it already germinates before it becomes detached from the anthers. So these data show much resemblance to what was observed for *C. hamulata*.

3. **C. palustris**

In the waterform of *C. palustris* we usually find fairly normally built flowers in the rosettes. The ♂ and ♀ flowers nearly always develop together in one leafaxil in this species (plate 14*c*; fig. 11*d*).

The stamina are small, but usually well developed, though the anthers do not always dehisce. The small globular pollengrains are also generally wellshaped for the greater part. The stigmata are erect-patulous, several times longer than the ovary, sometimes non-equal in size. As *C. palustris* generally habitates in places exposed to varying waterdepths and especially dessication, outspoken waterforms do not occur so often in nature. As a rule, after a longer or a shorter period transition- and landforms develop.

In the landforms the stigmata of the ♀ flowers are reduced to short stubs (plate 14*b*); the stamina are sometimes still extant, more or less clavate, in which yet a few shrivelled pollengrains may develop (plate 14*c*). Generally also this remainder is missing. Nevertheless fructification is abundant.

In literature we found the reduction of the ♀ flowers mentioned in "Flora des Puschlav" by BROCKMANN-JEROSCH (1907) only. The author found *C. palustris*-plants in the Puschlav area with "abortierten Narben", which however fructificated excellently.

Even if in well developed waterforms normal pollination is perhaps possible, in the landforms this way of reproduction must be considered out of the question owing to the reduction of stamens and stigmata. By anatomic and cytological investigation of the ovule it proved probable that in this landform apospory exists (cf. Ch. II).

CHAPTER V

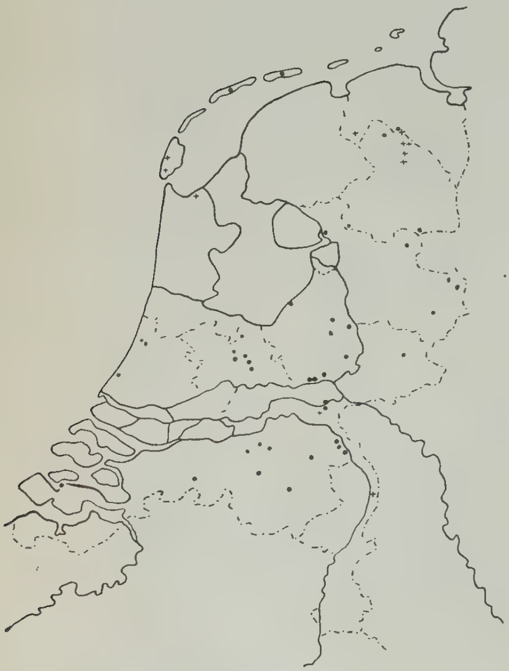
GEOGRAPHY AND ECOLOGY

1. **C. hamulata**

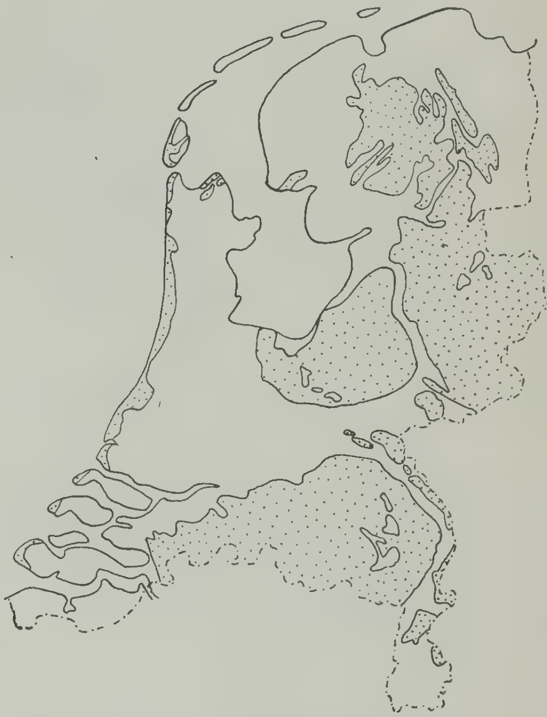
DISTRIBUTION (cf. appendix I, 1)

The Netherlands

According to the Dutch distribution map (map 1) *C. hamulata* is best represented in the provinces of Drenthe, Overijssel, the eastern part of Utrecht, Gelderland, N. Brabant and in a few Northsea-isles. This area seemingly shows but few peculiarities. If, however, we compare this map to a soilmap of the Netherlands (map 2), then it is striking that the localities of *C. hamulata* are situated on pleistocene sandy soils. Even in smaller, isolated pleistocene areas, as e.g. Vollenhove, Hippolytushoef, the country south of Nijmegen, the species occurs. In the province of Groningen, where we made many an investigation for *Callitriche*, it is only known to us from Marum, also



Map 1. C. hamulata. Distribution in the Netherlands (cf. app. I, 1).
• herb. specimens + living plants



Map 2. Sandy soils in the Netherlands (░). (Partly after MÖRZER BRUYNS and WESTHOFF, 1951).

situated in the pleistocene sandy part, and further from many finds to the south of the town of Groningen, all situated on the north elevations of the Hondsrug. In Drenthe *C. hamulata* a.o. occurs on the eastern slope of the Hondsrug. As for the provinces of North- and South-Holland we only know *C. hamulata* from the row of dunes of a few Northsea-isles and also from Loosduinen and Oegstgeest. These last localities are situated on sandy soil of the old dune landscape. In South-Limburg and on river clay soils and marine clay soils the species is entirely missing.

The water of these soils is generally neutral to slightly acid. The pH's of the localities reflect this (cf. appendix II, table I). The content of chloride is in most cases below 100 mg/L. Only a few findspots in Texel have a slightly higher percentage. Hippolytushoef forms an exception with 825 mg Cl′/L (cf. appendix II, table I). The extensive vegetation existing there makes us suppose that *C. hamulata* can also develop in oligohalinic water, though the germination of seeds in water of such Cl′ content did not succeed so far (cf. Ch. VI). The soils in which *C. hamulata* occurs are poor in lime.

Outside the Netherlands

As for the distribution abroad (map 6) there are several localities in Gr. Britain, France, Germany and Denmark. From Sweden we saw only a few herbarium specimina. According to Samuelsson—who described and determined *Callitriche hamulata* well—the species is especially common in the south, while he also gives several localities along the southern part of Norway's Westcoast.

From the Faer-Oer, Iceland, Finland, West-, South- and East-Greenland we saw several plants in the Copenhague herbarium. In Greenland *C. hamulata* occurs as far north as 68° 42″ N.L.

From Italy and Switzerland the materials were very scarce, while Poland, Austria and Czecho-Slovakia were not represented. Samuelsson too mentions but few localities in these countries. As the most easterly findspot of *C. hamulata*'s area he considers the Bohemian Wood. The plant found there is probably the specimen from the herbarium Delessert, which bears the determinationlabel of Samuelsson. Recapitulating we may say with Samuelsson that the European region—in so far as it is known at present—has a somewhat atlantic tendency. In the central European provinces it practically entirely confines itself to the western and northwestern part of the baltic sector. In the alpine sector there are only few localities.

Taking into consideration the existence in the continental parts of Scandinavia (Samuelsson), in Greenland and in Iceland, we certainly do not have to deal with a typical atlantic plant. From its appearing there it also becomes clear that *C. hamulata* is not limited to a climate with mild winters. Also in our country the species, usually a winter-annual, is very frostresisting. During a few consecutive years we observed that plants, grown into a layer of ice,—also floating—appeared fresh and green after the thaw had set in and normally went on growing.

As for the geological structure of the soil of the foreign localities we have at our disposal only a few data, noted down on herbarium labels. Thus *C. hamulata* specimina come from the Vosges, out of brooks across granite (e.g. the specimen from Gerardmer, dep. Vosges, h.Del.), which we observed in that country as well. Specimina from the Bohemian Wood (h.Del.) grew on gneiss, the plants in the Regnitz near Bamberg (a.o. h.Del.) on sandy soil. In Denmark the species occurs on pleistocene sandy soil. If we study the whole distribution area, it makes the impression that *C. hamulata* has a preference for poor soils. Calcareous soils it seems to avoid. So Samuelsson informs us that *C. hamulata*, in South-Sweden, is lacking in the calcareous cultural areas, as well as in the calcareous parts round the Oslofjord. In South-Limburg (cretaceous district) it was not seen either.

It moreover entirely tallies with our observations in the botanical garden "de Wolf" during the period from November 1952-August 1953, when it proved that as well land- as waterforms of *C. hamulata* developed badly in hollows with lime-marl. Most plants withered, a few remained very small with yellow leaves, while the plants in the neighbouring "cowpuddles" did very well in the normal soil or on a layer of peat. *C. stagnalis* and *C. platycarpa* showed a normal development on the marl.

Environment and Vegetation

The Netherlands

C. hamulata is found in the Netherlands mostly on a clean sandy soil in brooks (Arcen, Wolfheze, Loenen, Drenthe). Also in a swift current the plants can form dense vegetations with long floating stems. Sometimes we find *C. hamulata* in the brooks together with *C. platycarpa*. On the island of Texel we saw *C. hamulata* in flowing water in or along the dunes. It was further found in a few cattleponds with clear wellwater, not used as such however. In all this as good as oligotrophic water no other waterplants were found. In one cattlepond it grew together with *C. obtusangula* and *C. platycarpa* as landforms.

On the borders of the pleistocene, where the oligotrophic water mixes with the more eutrophic of the neighbouring area (Drenthe, eastern slope Hondsrug) we find *C. hamulata* in ditches with gently flowing to nearly stagnant water. Here the species grows in small clumps amidst an often dense vegetation of *Elisma natans* and *Hottonia*, sometimes with *Elodea* and *Menyanthes* along the edge. We may ask whether in this case instead of *C. palustris* from the Hottonietum palustris (Westhoff, 1946), not *C. hamulata* is meant. *C. palustris* in this association certainly never occurs. This biotically weak species requires quite a different kind of environment (cf. sub 5 of this chapter). In so far as we are now able to ascertain, the species *C. hamulata*, however, may be called characteristic for the Hottonietum.

In the botanical garden "de Wolf" *C. hamulata* occurred spontaneously and in great quantities during some years in two ditches with rainwater, not communicating with other watercourses. After the eutrophic water had however been drained off from the pond through these two ditches (1950) a quickly spreading vegetation of *Myriophyllum spicatum* appeared, while *C. hamulata* lost ground. Continually removing the *Myriophyllum*-plants was not able to prevent *C. hamulata* from disappearing nearly entirely from these ditches. Seeing that *C. hamulata* occurs in oligotrophic-mesotrophic water, the affluence of eutrophic water was probably primary for its vanishing, while moreover the species could not hold out against *Myriophyllum*.

C. hamulata is the only species of the Dutch Callitriche's that can live for years in water, poor in nutrients. In our indoor-cultures the plants proved to keep for years in rainwater, without its being refreshed. In these circumstances *C. hamulata* becomes perennial, so does not die in late summer, neither does it flower, but it remains a fresh green and grows on very slowly. Thus specimina, gathered in 1950 and in 1951, are still in our possession.

Outside the Netherlands

From abroad only a few data about the accompanying vegetation of *C. hamulata* are at our disposal. Moreover, it is often hard to discern whether the *Callitriche* was rightly determined, so that making use of such data might give rise to incorrect conclusions. Fairly reliable we consider the report of Nordhagen, mentioned by Samuelsson, concerning lower lake Sikkisdale on the western border of Central Norway. In this lake, situated at the height of 1000 m. in the birch-zone, *C. hamulata* occurred together with *Isoëtes lacustris*, *Sparganium affine* (sterile), *Potamogeton alpinus*, *Juncus supinus*, *Utricularia minor* and *Myriophyllum alterniflorum*.

Another, also oligotrophic community IVERSEN (1929) mentions from Praestesø, a "Heidesee", to the west of Varde in western Jutland. As became apparent from herbarium investigations *C. hamulata* is common in the surroundings of Varde. Besides this plant Iversen found in Praestesø: *Isoëtes lacustris*, *Sparganium affine*, *Scirpus fluitans*, *Juncus supinus*, *Elatine hexandra*, *Myriophyllum alterniflorum*, *Lobelia dortmanna*, *Littorella uniflora*, *Helosciadium inundatum*, *Potamogeton filiformis* and *Potamogeton crispus*. The water was neutral according to Iversen.

2. **C. obtusangula**

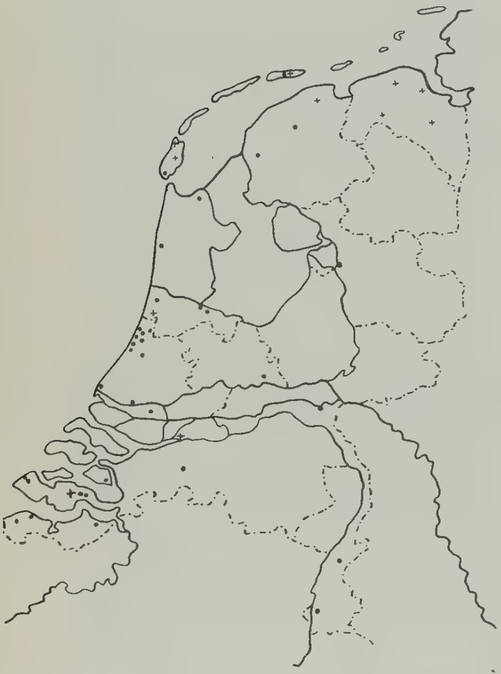
DISTRIBUTION (cf. appendix I, 2)

The Netherlands

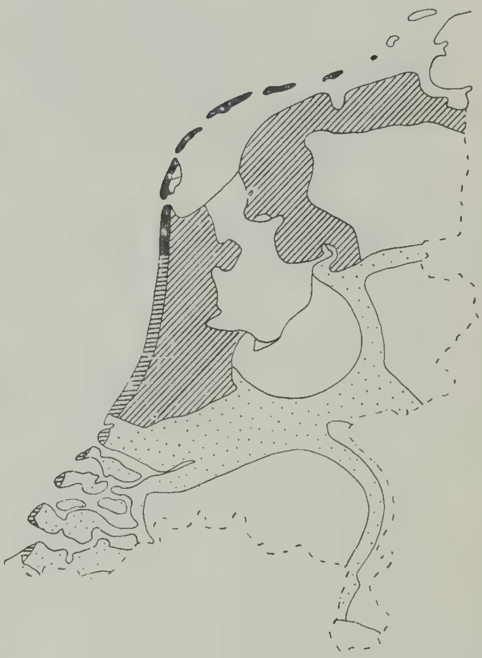
From the distribution map of the Netherlands (map 3) it appears that *C. obtusangula* only occurs in the wadden district, the haff district and the river district (map 4). In this last area it is especially found in the province of Zeeland; only here and there along the rivers are localities (Zwolle, Leersum, Ooypolder near Nijmegen, Amby, Roermond).

Outside the Netherlands

When studying the European herbarium data more closely we come to the conclusion, together with Samuelsson, that the geographical distribution is a mediterranean-atlantic one, radiating to the area round Geneva (map 5). That *C. obtusangula* also occurs in the cantons Geneva and Wallis, need not cause any surprise, as more mediterranean plants have forced their way into this country through the entrancegateway of the Rhonevalley (Weiss, 1934).



Map 3. C. obtusangula. Distribution in the Netherlands (cf. app. 1, 2)
• herb. specimens + living plants



Map 4. River-, haff-, wadden- and dunedistrict in the Netherlands (after Van Soest, Heukels en Wachter, Schoolflora v. Nederland).
░ River district ▨ Haff district
■ Wadden district ▤ Dune district

From N.W. Germany no localities are known to us, and in the herbarium at Copenhague no *C. obtusangula* from Denmark was present, so that we must take it for granted the species does not exist there.

In the northeast of the area, the northern Netherlands will form the boundary; to the west, in Great Britain, it is possible that it grows at a latitude yet a little heigher, in view of the data, giving a reliable-looking impression, in the British flora of CLAPHAM, TUTIN and WARBURG (1952) where they mention as localities a.o. Lancashire and York. We have however not yet seen herbarium specimens of this area.

C. obtusangula is a perennial. It continues to grow in winter with the aid of the submerged stems and continuously enlarges its area during this period.

In the mild rainy wintermonths of the area only a few days occur with a temperature below 0° C and it was to be taken for granted that this outspoken mediterranean-atlantic plant would not prove very frostresistant. Now the Groningen localities lie in an area with more than 11-12 icy days a year, while the frostperiod in Denmark averages about two months. It is very well possible that this lengthy frostperiod is the cause that *C. obtusangula* is absent from Denmark.

An indication that *C. obtusangula* is indeed susceptible to temperatures below 0° C, is to be found in the following observations in the botanical garden "de Wolf" during the winter 1952/1953. [1])

In the experimental brook there were also a.o. several extensive vegetations of *C. obtusangula* of Texel, the stems of which almost reached the waterlevel in the shallow parts. Already after a few icy days it became apparent how much more these plants were suffering than e.g. the interlying specimina of *C. stagnalis* and *C. platycarpa.* All leaved parts, becoming frozen, rotted after the thaw had set in. The stems, creeping in the mud, having had no contact with the ice, sprouted again nicely after the period of frost. Much damage was done to the floating plants; owing to the fact that they were entirely crusted with ice the damage was much greater than in the case of the rooted plants. After having produced a hesitating sprout all the test-plants succumbed in the spring. If we freeze *C. obtusangula* overnight in the refrigerator and thaw it during the day very gradually, at a temperature of a few degrees above 0° C, then we see a similar spectacle: the plants are quite black and limp after this has been done once or twice.

It is remarkable that *C. obtusangula* from Rottum (prov. of Groningen) showed hardly any frostdamage. The plants at issue were growing in two identical "cowpuddles" and quite filled them. Eight specimina from Texel grew under quite the same circumstances in the same area. On account of the shallowness of the water (about 10 cm.) the whole plant was sometimes almost covered by ice and this caused the already mentioned symptoms of perishing in nearly all specimina from Texel, after the thaw had set in. In the plants from Rottum, however, practically no damage could be found, nearly all the leaves remained a fresh green. Whether we have here a race with greater frostresistance or that an unknown incidental circumstance played us parts will have to be ascertained by further observations.

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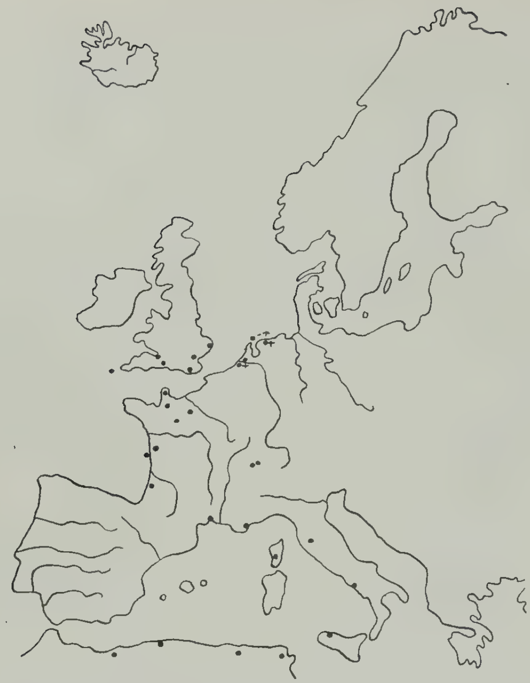
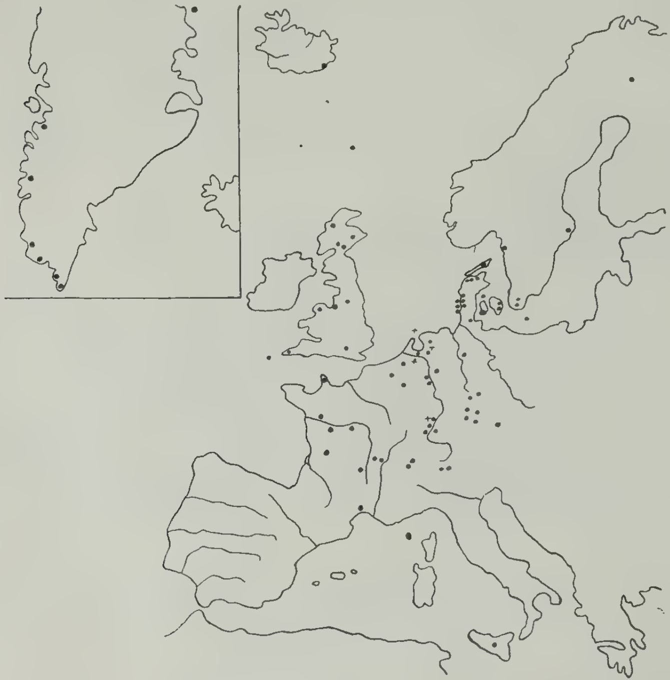
[1] In the winter of 1953/1954, when the frost penetrated to the bottom of the experimental brook, nearly the whole culture perished.



Map 5. C. obtusangula. Distribution in Europe and on the north coast of Africa (cf. app. I, 2). • herb. specimens + living plants



Map 6. C. hamulata. Distribution in Europe and Greenland (cf. app. I, 1). • herb. specimens + living plants

As was already observed (Ch. III) *C. obtusangula* resists desiccation much better than the other species. It maintains itself in the Netherlands as a landform; also in very sunny habitats. But data about its conduct during the dry warm summermonths in the mediterranean area are entirely wanting.

Environment and Vegetation

The Netherlands

In the ditches, in which we find *C. obtusangula* in the haff district of the Netherlands (prov. of Groningen, marine clay soils on the isle of Texel), we usually also find *Potamogeton pectinatus*, *Zannichellia palustris* ssp. *pedicellata*, *Enteromorpha intestinalis*, further *Lemna minor* and *L. trisulca*, *Phragmites*. In dried up mud of such ditches (a.o. the watercourse to the Slufter, Texel) there moreover often occurs a rich vegetation of *Scirpus maritimus* and *Schoenoplectus tabernaemontani*, between which a good sized vegetation of *C. obtusangula* landforms is to be found. Near den Hoorn on Texel, *C. obtusangula* was found in the spring of 1951 together with a smallflowering "Batrachium", which we identified as *Ranunculus tripartitus* DC. In the dune area of Texel we sometimes find *C. obtusangula* together with quite different plants, viz. *Hydrocotyle*, *Mentha aquatica*, *Echinodorus ranunculoides* etc.

The occurrence together with plants characteristic for brackish water, like *Zannichellia*, *Enteromorpha* (characteristic species of the alliance of Ruppion Maritimae Br-Bl) and *Scirpus maritimus* (characteristic species of Scirpetum maritimi Tx), besides the distribution in haff- and wadden district and the Zeeland part of the fluviatile area gave rise to the suggestion, that *C. obtusangula* is fairly salt-tolerant. Remarkable in this respect is the isolated locality Hoogkerk (prov. of Groningen) where in summer so much salt groundwater is present that a saltwater swimmingbath could be made and the cattleponds in the surroundings become unfit for use.

The water of the localities have a Cl′ content from 100 to about 2000 mg/L (cf. appendix II, table II). In ditches in or near the dune area of Texel the content of chloride may be less than 100 mg/L (samples 12, 18, 19). So these localities may be considered as appertaining to fresh water. From these facts we can gather that *C. obtusangula* is especially a plant of oligo-mesohalinic water. In the mesohalinic area it occurs together with *Zannichellia palustris* ssp. *pedicellata*, *Scirpus maritimus* etc.; in more oligohalinic water it can grow together with *Echinodorus*, *Hydrocotyle*, *Mentha aquatica*.

From the germination tests as well, described in Ch. VI, it appears that with a Cl′content of about 3000 mg/L the percentage of the germinating seeds is still high (71-88 %). Less common seems to be *C. obtusangula* in fresh water. It then principally remains restricted to the dune areas. In the freshwater cultures obstacles presented themselves. Only in a thick layer of ashes in the brook of the botanical garden "de Wolf" an abundant vegetation occurred.

The water of the localities is generally neutral-slightly alcalic (cf. appendix II, table II). *C. obtusangula* growing in Zuid-Beveland (prov. of Zeeland) differs from the other specimina found in the Netherlands in leafshape and in the presence of 2 SAT-chromosomes; it is stated in an environment richer in Cl′ than the plants from Texel and Groningen. According to VAN 'T LEVEN (1952 unpubl.) the Cl′ content can rise as high as 5000 mg/L in Zuid-Beveland. Also in cultures it is distinctly more salt-tolerant than *C. obtusangula* from Texel (cf. Ch. VI). We only call to mind here the fact that the seeds of the plants from Texel do not germinate in sol. 10 (6750 mg Cl/L). The seeds of the Zeeland plants however germinate abundantly in it.

Outside the Netherlands

In the west of France too and in the mediterranean area *C. obtusangula* grows in places comparable as for the vegetation with our brackish-water areas. In the department Morbihan e.g., where *C. obtusangula* was first described, grow a.o. *Triglochin barrelieri*, *Potamogeton pectinatus*, *Ruppia rostellata*, *Zannichellia dentata*, *Zostera nana*, further *Statice* sp., *Sonchus maritimus*, *Polygonum maritimum* etc. (LEGALL, 1852).

3. **C. platycarpa**

DISTRIBUTION (cf. appendix I, 3)

The Netherlands

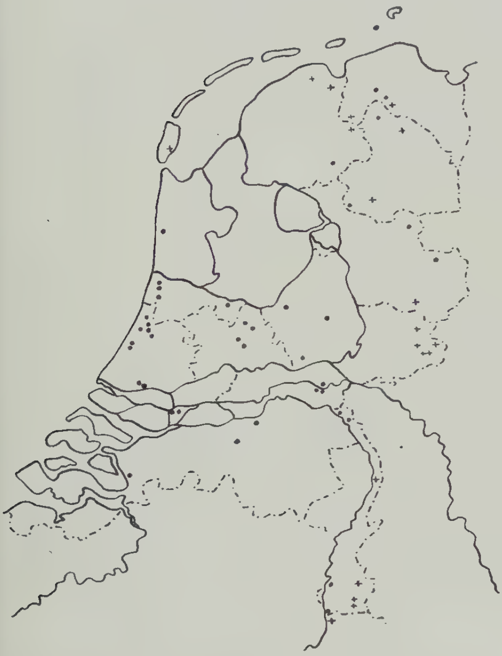
This species, new to the Netherlands, is remarkably enough the most common in the low lands. It occurs—except in Zeeland— in all provinces (map 7).

Because *C. platycarpa* is often gathered in sterile condition or with unripe fruits, numerous herbarium specimina cannot be identified with sufficient certainty. This is especially a handicap when fixing the foreign regions, for which one has entirely to rely on herbarium data. The temptation exists that one starts to identify plants solely by habit and leafshape—a temptation which some authors have not quite been able to resist—but, taking into consideration the great variability this cannot be justified for any specimen. Added to this is the drawback that in France plants, in all probability belonging to waterforms of *C. platycarpa*, show similarities with *C. stagnalis* in fruitform and sometimes also in habit. Samuelsson met with the same difficulty in his researches. It is very well possible that other climatological circumstances and other soil structure cause such a modification, but it is just as well possible that here a genetically differing form is concerned, which can only be stated by cytological research and culture experiments. As this was not possible so far, these dubious plants were not noted down on the distribution list.

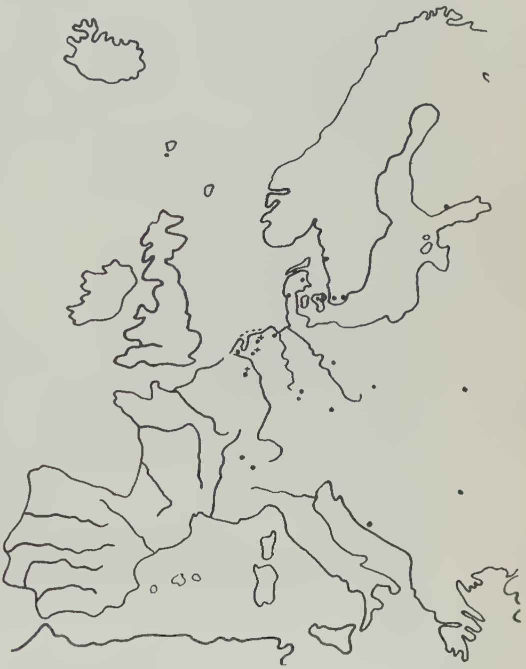
Outside the Netherlands

Most findspots out of the Netherlands lie in Germany and Denmark. Further *C. platycarpa* occurs in Sweden, here and there in Switzerland and Czecho-Slovakia. From Finland, western Russia and a few

Balkan countries there were some plants in herbaria. In the Iceland and the Greenland herbarium material *C. platycarpa* was not found. Neither in the higher parts of the Alps does it seem to grow, which Samuelsson also tells us. It gives an impression that it habitates the lower regions in Europe (map 8).



Map 7. C. platycarpa. Distribution in the Netherlands (cf. app. I, 3).
• herb. specimens + living plants



Map 8. C. platycarpa. Distribution in Europe (cf. app. I, 3).
• herb. specimens + living plants

ENVIRONMENT

The Netherlands

In the Netherlands we find *C. platycarpa* in stagnant water and in flowing, on sandy soils, clay soils and on the calcareous soils of Zuid-Limburg. In the field it is a freshwater plant, also in the coastal range it rarely occurs in water which a Cl′ content higher than 100 mg/L (cf. appendix II, table III). In that case it sometimes grows together with *C. obtusangula* (Haarlem, Dokkum, Oude Schild in Texel). The species is missing from Zeeland and from the typical brackish parts of the haff- and wadden district.

The pH in the series of samples varied from slightly acid to slightly alcalic (cf. appendix II, table III).

As to the richness in nutrients of the water, we find *C. platycarpa* mostly in mesotrophic-eutrophic water, together with *Elodea, Ceratophyllum submersum* (shallow water) and sometimes with *Myriophyllum* *spicatum*, *Potamogeton natans* and *Nymphaea alba* (at the edge of deeper water). Even in polluted water *C. platycarpa* can subsist (ditches along farmhouses). Nevertheless the species is also found in oligotrophic water on clean sandy soils (a few places near Haren, eastern part of Gelderland, the Veluwe and northern Limburg). It may then grow together with *C. hamulata*. Also in calcareous areas we can find *C. platycarpa* (Zuid-Limburg, Belgian side of Sint Pietersberg).

Whether the specimina from brooks (only to be cultivated further in flowing water) represent another ecotype, must be investigated more closely.

Resuming we may say that *C. platycarpa* gives an impression of being a freshwater plant in the lower regions of Europe, where it proves to be fairly ubiquist.

4. **C. stagnalis**

Distribution (cf. appendix I, 4)

The Netherlands

This species does not seem to be very common in our country. We found it in the brookvalley area near Schipborg (prov. of Drenthe) and near Lieveren (ib.). Further living material was produced from the Biesbos (prov. of Zuid-Holland and Noord-Brabant). From the surroundings of this latter area there were also several herbarium plants. The other herbarium data originate principally from brookvalley areas (Coevorden, de Lutte, Renkum, Ruurlo) and from places along the big rivers (Utrecht, Vreeswijk, Nijmegen, Middachten, Leiden, map 9). From the marine clay areas, from peat soils and from Limburg no findspots are known. Interesting is the recent find of Reichgelt in Terschelling, one of the very scarce *C. stagnalis* localities on our Northsea-islands. It was to be expected there, as *C. stagnalis* is common on Denmark's westcoast and also occurs in Borkum, but neither in Texel nor in Ameland did we succeed in finding specimina of the species.

Outside the Netherlands

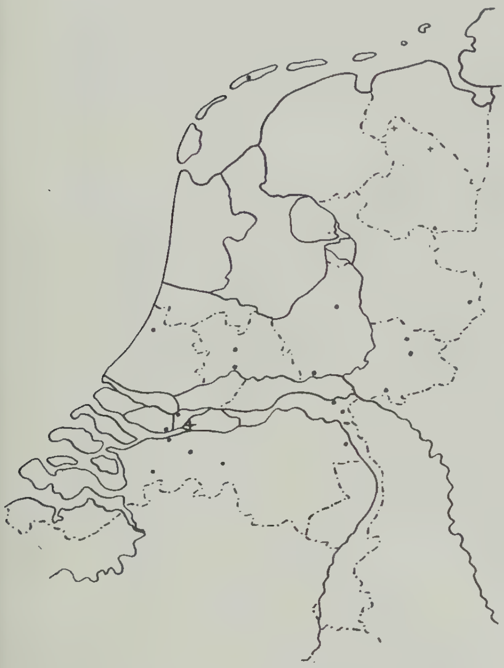
As for the other countries of Europe, we saw herbarium material from Sweden, Norway, S.W. Iceland, the Faer-Oer, Great Britain, France, Portugal, Spain, Italy, Switzerland and Germany (map 10).

Also in those countries *C. stagnalis* often occurs along the coast or near estuaries (Trondheim, Göteborg, Rörvig, coast of Jylland, Manche, Nantes, Vendée, Oléron, Bordeaux, Bastia, Ajaccio, Espinho, N. coast of Spain, Minorca, Venice, Messina, Bremen, Rügen, Borkum, Cumberland and Somerset, coast Faer-Oer, S.W. coast of Iceland). Inland it occurs in rivervalleys (Paris, Epinal, Toulouse, Coimbra, Rheinfelden, Cleve, Padova), in brookvalleys (Schleusingen). Here and there it occurs at greater height, as in the Haute Savoie and in Switzerland, but principally along the lakes there (Lac Majeur, Lac de Muzzano, the Lake of Geneva).

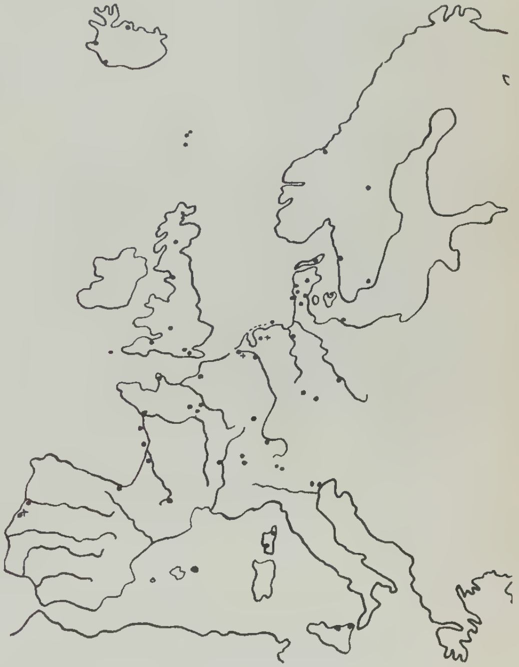
Environment and Vegetation

About the factors of the environment of the habitats of *C. stagnalis* little is as yet known, the same holding good for the accompanying vegetation of plants.

In the Biesbos it grows in the mud of creekbanks in the "kleine kreekoever gezelschap"1) belonging to the Sparganion. It further grows in tidal woods (Alnion).1) In a few cases it appears here together with *C. obtusangula*. In France and Great Britain this is the case too.



Map 9. C. stagnalis. Distribution in the Netherlands (cf. app. I, 4).
· herb. specimens + living plants



Map 10. C. stagnalis. Distribution in Europe (cf. app. I, 4).
· herb. specimens + living plants

In the brookvalley area in Drenthe *C. stagnalis* was found in the "cowpuddles" and furrows together with *C. palustris*, *Stellaria uliginosa* etc. (cf. vegetation-description *C. palustris*). Once a rich vegetation was found in a dystrophic ditch in the brookvalley near Schipborg, while *C. stagnalis* also flourished on a damp path near Lieveren. In Terschelling it appears in brackish water with *Zannichellia palustris* ssp. *pedicellata* (in sched. Reichgelt, 1951).

As regards the distribution of plants differing in cytological respect, we still have at our disposal too few data. It could be ascertained that the plants, found in Lieveren, have 2 SAT-chromosomes just

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[1] Ir S. Sonneveld by letter.

like those from Middachten. In Schipborg plants occur with 0,1 or 2 SAT-chromosomes.

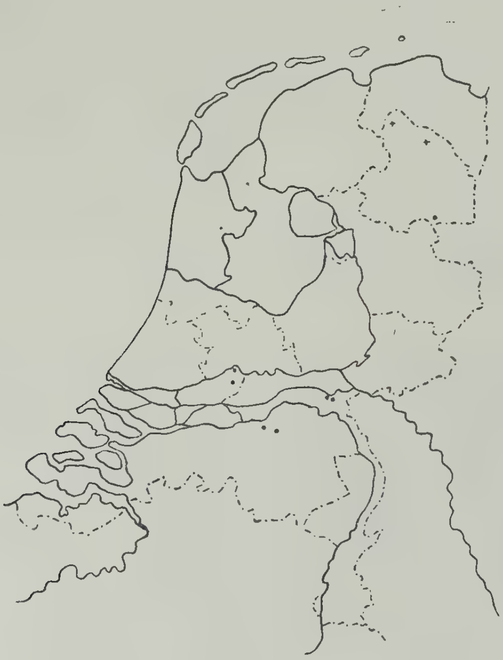
C. stagnalis, and *C. obtusangula* likewise, proves much more salt-tolerant than *C. hamulata* and *C. platycarpa*, which tallies with its appearance along the coast. Of the seeds from Coimbra even 100 % germinated in solution 3 (cf. Ch. VI). Generally speaking *C. stagnalis* seems to us a plant especially occurring in rivervalleys, estuaries and—at greater height—along lakes.

5. **C. palustris**

Distribution (cf. appendix I, 5)

The Netherlands

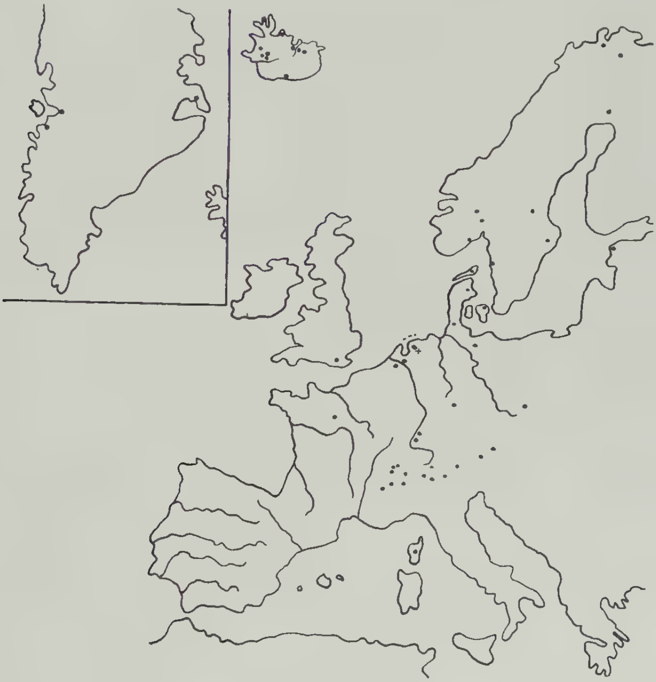
This interesting plant grows in only a few places in the Netherlands. From Berlicum and the surroundings of 's Hertogenbosch (prov. of N. Brabant) about the middle of last century extensive material was brought together by a certain Van Hoven, which is among the best gathered of this species in the Netherlands. Further there were plants in the Leiden herbarium from Heikop near Vianen, Persinge near Nijmegen and from Coevorden. We ourselves found a few scattered landforms in the valley of the Lieveren brook and a fairly rich habitat near the Schipborg brook (map 11).



Map 11. C. palustris. Distribution in the Netherlands (cf. app. I, 5).
· herb. specimens + living plants

Outside the Netherlands

In the lower regions of France, Germany and Switzerland the species also occurs sporadically: in Denmark, Sweden and Finland it neither seems to be common. Especially the Alpine sector, however, is remarkably abundant in finds, just as Iceland and Greenland (map 12). As for the former area, we mention, in France, the departments Doubs, Isère and especially Savoie and Haute Savoie; in Switzerland the cantons Vaud, Valais, Graubünden, Tessin and Bern have many localities, while there were herbarium specimina from Linz, Salzburg and Tirol in Austria. In Italy *C. palustris* occurs in the alpine part (Alpes bergamasques etc.).



Map 12. C. palustris. Distribution in Europe and Greenland (cf. app. I, 5).
• herb. material + living plants

Often it grows at great height. Thus *C. palustris* rises above 2500 m. in the Alps (Braun-Blanquet, in sched.).

In Iceland too *C. palustris*—considered the numerous specimina in the Copenhague herbarium—is fairly frequent. The same holds good for Greenland. The most northern findspot lies here at 71° N.L.

The area of *C. palustris*, however, is not limited to the above-mentioned arctic-alpine area. Sokolovskaja (1932) gives us several localities in Russia, among which the Caucasus is well represented. In Asia *C. palustris* is especially found in the mountains about the 50th degree of latitude, between about 60° and 110° N.Longitude (a.o. the Altairegion). We ourselves saw Asian herbarium plants from Siberia, Kashmir (N.W. Himalaya), Yunnan, the upper course of the Amur, Japan, Corea and Taiwan (Formosa). Also in N. America *C. palustris* occurs (a.o. Labrador). As in Eastern Europe and Asia plants occur with slightly diverging fruitform (PETROV, 1928) we shall not treat this part of the area further.

ENVIRONMENT AND VEGETATION

The Netherlands

The growth of *C. palustris* is restricted to very special conditions of environment. On account of its frail habit it cannot stand swift watermovement as waterform, as also appeared from transplant experiments in the experimental brook of the botanical garden "de Wolf" (Ch. III). The stems are short and the branching is but little, it does not form any dense vegetation of quickgrowing clumps, like some of the other species. Its appearance is usually of an ephemerous character, though in a single case a dense vegetation may occur by an accrescence of seed on a small plot. As it proved from cultures and fieldobservations, *C. palustris* as waterform depends on scarce, shallow quantities of stagnant water. The germination of the seeds too takes place exclusively under such conditions; probably in shallow water the temperature can rise quickly in spring to the value necessary for germination (about 20° C, exper. unpubl.).

As landform it rarely forms a dense vegetation, contrary to *C. platycarpa* and *C. hamulata*; the little plants usually grow scattered. Owing to its frail growth it is much more dependent than the other species on a clear substrate when germinating and for further development, where—at least during its vegetation period—no coarse, quickly growing plants occur.

In the Netherlands *C. palustris* occurs only in the brookvalleys of Drenthe in "cowpuddles" and tiny furrows in the marshy strip of land, flooded in winter, along the banks of the brooks. Usually these strips are used as pasture, and many parts are mown as well. According to the waterlevel the plant occurs here as land- or waterform, usually accompanied by *C. stagnalis* and small herbs like *Stellaria alsine*, *Peplis portula* and sometimes by *Montia*. In a few cases a specimen of *C. hamulata* and *C. platycarpa* is found. Further we meet in this vegetation here and there, *Ranunculus flammula*, *Myosotis palustris*, *Galium palustre*, *Alopecurus geniculatus* and *Rorippa islandica*.

At the end of *C. palustris*' vegetation period a Polygoneto-Bidentetum cernui develops in late summer in many places, in which especially *Polygonum hydropiper* and *Bidens tripartitus* occur. Perhaps the disappearance of *C. palustris* is somewhat hastened by this compact, quickly growing vegetation, though also in areas free of rivalry most *C. palustris*-plants perish about August-September.

If an important change in waterlevel or growth of plants takes place, the development of *C. palustris* is immediately hampered. Such a case occurred in 1953 near the Schipborg brook. Owing to the quantity of rain the area along the brook remained flooded nearly all summer. In the localities of the foregoing years the water reached to more than half a meter high, so that pasturing was not possible. Neither could the grass be mown, so that a dense vegetation of Gramineae with long leaves, decaying here and there, filled the former furrows and "cowpuddles". Only in the shallow zone, in a few small plots with a clean substrate a few *C. palustris*-plants appeared; in the deeper parts nothing could be discovered. The thick growth of grass and the deep water—owing to which the temperature remained too low on the bottom—had most probably already prevented the germination of the seeds.

In N. Brabant *C. palustris* occurred according to Van Hoven (in sched. 1847) along the Dommel and in the hollows along the river A, near 's Hertogenbosch. It is remarkable that the species appeared spontaneously and abundantly in the botanical garden "de Wolf", where "cowpuddles" had been artificially made in the marshy area along the experimental brook in the spring of 1953 and in a shallow little pool.

All Dutch localities lie in freshwater regions. As the species occurs but rarely, we have a wateranalysis of but one locality, besides that of the habitat in the botanical garden "de Wolf". (cf. appendix II, table IV).

Outside the Netherlands

An environment analogous to the "cowpuddles" in the brookvalleys described above, is found in Finland. In his interesting ecological study about the South Finnish skaror area LUTHER (1951) relates that *C. palustris* occurs here in "Hufspuren", "Ruderstrassen" and "Bootufer". The "Hufspuren" are here situated along the edges of the swampy meadows, adjoining the reedborder along the coast. On the landing-places and in the paths the boats have forced through the reed vegetation—where the bottom is practically clean—*C. palustris* principally grows together with other biotic weak species, as *Subularia aquatica*, *Ranunculus confervoides*, *Crassula aquatica*, *Elatine hydropiper* and *triandra*, *Limosella aquatica* and some *Chara*- and *Nitella*species.

As well from the Dutch observations as from Luther's description it becomes apparent that the existence of *C. palustris* in culture areas is strongly dependent on human influence. It can only maintain itself in habitats, where on account of the continuous eliminating of the existent vegetation small areas with clean substrates originate. It is probable that also in the marshy hayfields in Iceland *C. palustris* grows under analogous circumstances.

In rocky regions (a.o. in Finland) and in mountain areas *C. palustris* is especially a plant of "Felstümpel", puddles in drying river beds, glacier regions (Rhoneglacier) etc.

In the Alps it sometimes forms a "Verlandungspioniergesellschaft" with *Sparganium affine*, *Rorippa islandica*, *Ranunculus flaccida* and *Alopecurus aequalis*, in drying puddles (Braun-Blanquet in sched.). In Iceland it grows a.o. on the "hraun" (lava) in and near the brooks and besides in the Geysir together with Cyanophyceae (h.C.).

Chapter VI

INFLUENCE OF SALTISH WATER ON THE GERMINATION OF THE SEEDS

For *C. hamulata*, *C. obtusangula*, *C. platycarpa*, and *C. stagnalis* the germinative power in saltish water was studied. The seeds were sown in petridishes, in artificially composed diluted seawater of different strenghts (Bakker 1951).

The solutions contain per l:

sol. 1 = 1 g NaCl + 0.12 g $MgCl_2$ + 0.08 g $MgSO_4$ + 0.05 g $CaSO_4$ + 0.02 g KCl.
sol. 2 = 3 g NaCl + 0.36 g $MgCl_2$ + 0.24 g $MgSO_4$ + 0.15 g $CaSO_4$ + 0.06 g KCl.
sol. 3 = 5 g NaCl + 0.60 g $MgCl_2$ + 0.41 g $MgSO_4$ + 0.24 g $CaSO_4$ + 0.11 g KCl.
sol. 4 = 10 g NaCl + 1.20 g $MgCl_2$ + 0.82 g $MgSO_4$ + 0.49 g $CaSO_4$ + 0.22 g KCl.

The Cl′content is as follows (analysed in the same way as the field samples, Ch. V):

TABLE V

Sol. nr.	Content of Cl′ in mgr/L
1	680
2	1970
3	3400
4	6750

1. **C. hamulata**

Seeds from plants growing at Haren (Gr.)
No germination occurred for this species in the solutions used.

2. **C. obtusangula**

A. Seeds from plants growing in Texel

The tables indicate the percentage of germinated seeds, a fortnight after having been sown.

TABLE VI
Sown 29-7-'53. Number of seeds for every solution 25.

Sol. nr.	Perc. of germ. seeds
1	95
2	96
3	88
4	—

TABLE VII
Sown 10-8-'53.
Number of seeds for every solution 25.

Sol. nr.	Perc. of germ. seeds
1	96
2	81
3	71
4	—

TABLE VIII
Sown 10-8-'53.
Number of seeds for every solution 100.

Sol. nr.	Perc. of germ. seeds
1	97
2	81
3	77
4	—

B. Seeds from plants growing in Zuid-Beveland (Zeeland)

TABLE IX
Sown 29-8-'53.
Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	98
2	99
3	97
4	97

TABLE X
Sown 15-9-'53.
Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	99
2	98
3	99
4	95

3. **C. platycarpa**

Seeds from plants growing at Haren (Gr.)

As *C. platycarpa* germinates best in fresh water after the seeds have been subject to a low temperature during a short period (experiments unpubl.), the sowing experiment was made in salt solutions at different temperatures.

The tables indicate the percentage of germinated seeds, a fortnight after having been sown.

TABLE XI
Sown 9-10-'53. Temp. 12° C.
Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	14
2	2
3	2
4	—

TABLE XII
Sown 9-10-'53. The seeds were stored at a temperature of 12° C. After having been sown in the petridishes, these were placed in a room at a temperature of 25° C. Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	46
2	0
3	2
4	1

TABLE XIII
Sown 9-10-'53. The seeds were put in the refrigerator for 1 week at a temperature of —4° C. After having been sown in the petridishes, these were put in a room at a temperature of 25° C. The table indicates the percentage of germinated seeds after 1 week. Number of seeds for every solution 50.

Sol. nr.	Perc. of germ. seeds
1	99
2	17
3	1
4	—

4. **C. stagnalis**

As the number of seeds from Dutch material at our disposal was too small, seeds of plants from the botanical garden of Coimbra (Portugal) were used.

In each solution 50 seeds were sown.

TABLE XIV
Sown 15-5-'53.

Sol. nr.	Perc. of germ. seeds		
	24 May	25 June	1 July
1	100	100	100
2	100	100	100
3	0	61	100
4	0	9	died

TABLE XV
Sown 26-6-'53.

Sol. nr.	Perc. of germ. seeds		
	2 July	12 July	25 July
1	99	100	100
2	100	100	100
3	0	24	100
4	0	2	died

5. **C. palustris**

As too few seeds were at our disposal, no experiments were made for this species.

From the aforegiven tables it becomes clear that the germination may, for some species, take place in a much higher saltconcentration than for others. Thus the germination-percentage in sol. 3 is still very high for *C. stagnalis* and *C. obtusangula* (material from Texel), while for *C. platycarpa* only in sol. 1 a high percentage is reached under the most favourable circumstances.

For *C. hamulata* the seeds did not germinate even in sol. 1, while in rainwater always abundant germination occurred.

With a view to the germination *C. hamulata* is therefore probably the least salt tolerant of the species mentioned above, which tallies with the data about the Dutch distribution area, from which it proved that *C. hamulata* grows in fresh water (cf. Ch. V).

C. platycarpa can stand a higher saltconcentration, but as in sol. 2 only 17 % of the seeds germinated, the normal development will take place up to a value of a Cl′ content of ± 1000 mg/L.

From the distribution in the Netherlands it appeared that *C. platycarpa* also is predominantly a freshwater plant. In the wadden- and haff districts it occurs in oligohalinic water at best.

As regards the germination of the seeds of *C. obtusangula*, there is a distinct difference between the material from Zeeland and that from Texel. If we compare the tables VI, VII, and VIII (Texel) with IX and X (Zeeland) then we see that in the first three cases in sol. 3 the percentage of germinated seeds is a little lower than in sol. 1 and 2, while in sol. 4 no germination occurs anymore. The seeds of the Zeeland plants on the contrary germinate also in sol. 4 in a percentage nearly as high as in the other solutions.

C. obtusangula growing in Zeeland is therefore clearly more salt-tolerant than the plants from Texel, which also manifests itself in the Cl′ content of the findspots, lying much higher in Zuid-Beveland than in Texel (cf. Ch. V).

In *C. stagnalis* (Coimbra) all seeds still germinate in sol. 3, according to tables XIV and XV. So it can stand a Cl′ content of 3400 mg/L quite well and will still be able to develop well in brackish water. That is what its occurrence along the coasts and in the estuaries point to (cf. Ch. V).

Chapter VII

NOMENCLATURE

1. **C. hamulata** Ktzg

This name dates from 1837 and was published by Kützing, in Koch (1837). In Reichenbach (1841) some clear reproductions were given.

He had already earlier given good descriptions and reproductions of the species (1831 and 1832), under the name of *C. autumnalis* L. however. He thought that forms of his new species were part of *C. autumnalis* L. and he obviously wished to make a division, giving the name *C. autumnalis* L. to his species, while he started indicating the rest of the original species of Linné by the name of *C. virens* Goldbach. According to Kützing *C. autumnalis* L. sensu L. therefore comprised, besides *C. autumnalis* L. sensu Ktzg (the later *C. hamulata*), also *C. virens* Goldbach (*C. autumnalis* L., *C. hermaphroditica* Juslen., cf. sub 5).

In 1837 Kützing changed the nomenclature, originally chosen by him, in this sense that he again connected the name *C. autumnalis* to that part of the Linnean species that we even now know as *C. autumnalis* L. (*C. hermaphroditica* Juslen.), while he gave the rest, corresponding with his own species, the new name *C. hamulata* Ktzg.

In literature we sometimes find as a synonym for *C. hamulata* Ktzg the name *C. intermedia* Hoffm. (not intermedia Schkuhr, as Wahlenberg mentions in his Flora Lapponica, 1812). *C. hamulata* is also sometimes considered as a variety of *C. intermedia* Hoffm. (a.o. in the British flora by Clapham, Tutin and Warburg, 1952).

C. intermedia was described by Hoffmann in the "Bot. Taschenb. f. d. Jahr 1791". Here the author refers to Schkuhr, Bot. Handb. t. 1 (1791) fig. e. This fig. e refers to a twig of *Callitriche* that Schkuhr indicates by the name *C. autumnalis* (in his text; below the picture, only *C. verna* is mentioned accidentally; fig. 6).

This twig surely does not represent *C. hamulata*, but it is quite a different *Callitriche* which becomes apparent from the upright stamens in the rosettes. Such stamens do not occur in *C. hamulata* (cf. Ch. IV).

Therefore *C. intermedia* Hoffm. should in no way be connected with *C. hamulata* Ktzg.

2. **C. obtusangula** Legall

In his "Flore du Morbihan" of 1852 Legall mentions a new *Callitriche* he had found in the departments Ille-et-Vilaine and Morbihan. According to him the plant resembles the "Callitric des

étangs (C. stagnalis), mais il en diffère par le fruit dont les loges ne sont point en carène ailée, mais présentent un dos très obtus. C. obtusangula N."

The description is not extensive, but by the characteristics mentioned of the fruit, the plant is well designated, so that it is quite clear which *Callitriche* Legall meant. His localities as well fit in perfectly with the area as we know it now for the *C. obtusangula*.

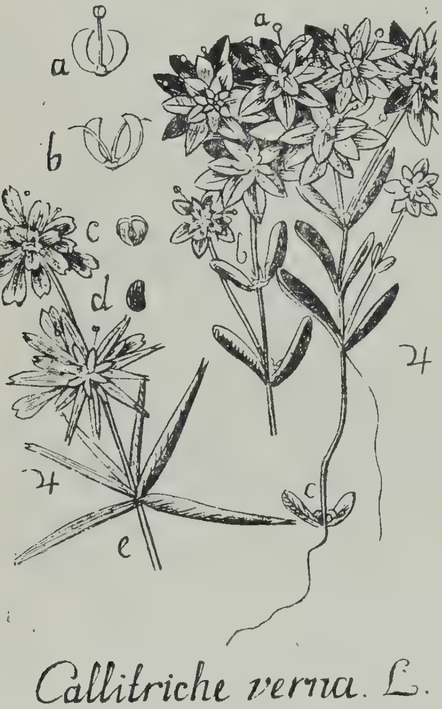


Fig. 6. After Schkuhr (1791). On the left Hoffmann's C. intermedia. For explanation see text.

About the taxonomic rank which the new *Callitriche* would have to occupy, Legall probably was still somewhat uncertain, as becomes clear from the sentence: "c'est au moins une var. fort remarquable du Callitric des étangs."

He however used the name obtusangula as a specific epithet in the diagnosis and this fact seems sufficient for us to consider the specific name *C. obtusangula* Legall as validly published.

3. **C. platycarpa** Ktzg

In 1831 Kützing described a new species of *Callitriche*, common in Germany, which he gave the name *C. platycarpa*. This species, according to him, somewhat resembles *C. stagnalis* but diverges vegetatively by the linear young leaves, linear stem leaves and the absence of branches directly under the rosette. Kützing most emphatically states here that *C. stagnalis* remains the most constant in leafshape of all species under varying conditions and never shows linear leaves.

Further, according to the description, the fruits of *C. platycarpa* are a little smaller than those of *C. stagnalis* and the carpels are less divergent. If we study the reproductions in REICHENBACH's Iconogr. bot. 1831 (tab. DCCCLXXXIII-DCCCLXXXIX), in Ic. fl. germ. 1841 (tab. CXXIX, fig. 4748) and the herbarium material collected by Kützing (h.L.), then there is no doubt but that Kützing meant by *C. platycarpa* the species, also most common in the Netherlands. As Kützing's *C. platycarpa* is the oldest validly published name for this species the Callitriche at issue will have to bear the specific epithet platycarpa. This species is new for the Netherlands.

From the beginning there has been great confusion roundabout *C. platycarpa* in Europe. By some authors (a.o. Lebel) the name *C. platycarpa* was used for *C. stagnalis*-plants, others considered *C. platycarpa* as *C. verna* L. or distinguished a variety platycarpa of *C. stagnalis*; also for *C. platycarpa* pro parte the name *C. polymorpha* Lönnr. was used. This was first done by SAMUELSSON (1925), who tried to escape from the confusion by entirely rejecting the name platycarpa. He was of opinion that Kützing had not rigthly outlined his species: *C. platycarpa* was thought to be composed of a heterogeneous group of bigfruited and smallfruited plants. Now Samuelsson regarded all bigfruited specimens as belonging to *C. stagnalis*, for the smallfruited plants he used the name *C. polymorpha* Lönnr.

The problem, however, was not solved in this way. In the first place the above-mentioned changing of nomenclature is not permitted according to int. code nom. 1952, art. 63. In the second place it does not show either in Kützing's descriptions, or in his reproductions, that he really brought together plants with very different-sized fruits in the species *C. platycarpa*. Now, what must we understand by *C. polymorpha* Lönnr. mentioned by Samuelsson? Is it indeed identical with the smallfruited *C. platycarpa* growing under special circumstances?

C. polymorpha was described in 1854 by LÖNNROTH and was common in Sweden. If we compare the diagnosis with that of the *C. platycarpa* Ktzg, then it proves that there exists an important difference in the size of the fruits. Also the width of the wings is different.

Lönnroth says of his plants: that the fruit is "aequi longi, ac fructus (sunt) C. vernae, paullo latiores et crassiores, . . . marginibus carpellorum . . . obtusis, vix alatis." Kützing, however, describes the fruits of his *C. platycarpa* as being somewhat smaller than those of *C. stagnalis*.

Lönnroth, acquainted with Kützing's description, was also struck by this fact. He says a.o.: ". . . C. platycarpa Kütz., cujus formam typicam Reich. icon. 1189-90 exprimunt, fructibus differt multo maioribus, cartilagineo alatis, longitudine paene latioribus." Lönnroth considered his plants, a.o. owing to the fruitshape, as a species different from *C. platycarpa*.

In Swedish herbarium material we indeed found plants as described by Lönnroth (a.o. ex. herb. Svanlund, h.G.). In the Netherlands such plants were not observed thus far. In the very variable *C. platycarpa* under certain circumstances specimina occur with fruits smaller than normal, while also the width of the wings may vary. But they are too different from the Swedish plants for us to call the *C. polymorpha* a mere modification or var. of *C. platycarpa*.

Only by cytological investigations and culture experiments we shall be able to ascertain whether *C. polymorpha* is a species or a—perhaps northern—form or variety of *C. platycarpa*.

The chromosome number $2n = 12$ (*C. platycarpa* has $2n = 20$), stated by Löve and Löve (1948), might perhaps point towards a species. The analogy in habit and pollen shape may speak for the second possibility.

4. **C. stagnalis** Scop.

C. stagnalis was described in 1772 by Scopoli in his "Flora carniolica" as follows: "Folia ovata. Flores polygami. Habitat in fossis circa Tergestum, aqua marina plenis." He further refers to Stellaria 3 in Haller's Enumeratio (1742), where we find the following words: "3 Stellaria foliis omnibus subrotundis".

Though both diagnoses are not very ample, it is sufficiently clear which species Scopoli meant. The "foliis omnibus subrotundis" from Haller's diagnosis is characteristic for this species, the only one in Europe that never bears linear leaves (cf. Ch. III and VIII). Further, the findspot Triëst, as well as the occurrence of the plant in salt water there, is quite in accordance with our data about the distribution area and the salt tolerance (cf. Ch. V and VI).

The mentioning of "Flores polygami" (so unisexual as well as hermaphrodite flowers) moreover indicates that Scopoli has very accurately observed that in his species a ♂ and a ♀ flower may occur together in one leafaxil. He, however, apparently considered the two flowers as one hermaphrodite flower, as was done by many authors.

5. **C. palustris** L.

The nomenclature of this species has given rise to much misunderstanding. The cause of this is, among other things, the fact that in the days of Linné the nomenclature of *Callitriche* was changed three times in the course of a few years, while the descriptions were little accurate.

If we trace the nomenclature of Linné and his pupils chronologically, then we get the following survey.

In Spec. pl. ed. I 1753 Linné describes one species, viz. *C. palustris*, with the varieties minima, β bifida and γ natans.

In 1754 Grufberg (Fl. angl.) and Hedenberg (Stat. Plant.) also speak of *C. palustris*. In February 1755 the Cent. I Plant. of Juslenius appeared, in which he describes 2 Callitriche species viz. *C. androgyna* and *C. hermaphroditica*. Paying attention to the references in the descriptions we presume that *C. hermaphroditica* took the place of *C. palustris β bifida*, while *C. androgyna* is probably *C. palustris* (α) *minima* and *C. palustris γ natans*, joined together. In October of the same year we find in the 2nd ed. of the Flora suecica, two other names. Linné now distinguishes *C. verna* and *C. autumnalis*, the description of which nearly entirely falls in with resp. *C. androgyna* and *C. hermaphroditica* of Juslenius. Why he changed Juslenius' nomenclature he doesn't say. In the following years NATHORST (1756) uses the names of Juslenius, while HOLM (1757) again takes the names *C. verna* and *C. autumnalis*, curiously enough with the indication "N".

In the Spec. pl. ed. II, 1762 (citation) and in ed. III, 1764 LINNÉ maintains his *C. verna* and *C. autumnalis*, and also uses this nomenclature in his herbarium.

Now, which Callitriche's were indicated by the names mentioned above? The descriptions do not make us much wiser and therefore SAMUELSSON (1925) presumed that by *C. hermaphroditica* (*C. autumnalis*) only submerged Callitriche's were meant and by *C. androgyna* (*C. verna*) landforms and rosette-bearing plants. If, however, we study the herbarium of Linné, then it does not seem improbable that by his *C. verna* and *C. autumnalis* he most certainly meant two definite species.

On the first sheet (plate 15) we find, below an undetermined, sterile *Callitriche* two specimina, indicated by the name *C. autumnalis*. Both indeed belong to the species of the section Pseudo-callitriche, which we nowadays indicate by that name or by *C. hermaphroditica*. Samuelsson's supposition that Linné meant another Callitriche by *C. autumnalis* and did not know this Pseudo-callitriche, proved wrong, on account of the existence of these two plants.

Further three waterforms have been gathered under the name of *C. verna*, while under the same name, on a second sheet, six small landforms are present. All these specimina with their conspicuous small fruits belong to one species, which—outlined more or less exactly—is now indicated by most authors by this name (or by *C. vernalis* Ktzg,[1]) *C. androgyna* Juslen., *C. palustris* L.).

That Linné did not provide the topmost Callitriche on the first sheet with a name, might also show that the division C. *verna* - *C. autumnalis* is not only based on modifications, as Samuelsson suggested. If this were the case, this specimen would probably have been classed with one of the two species.

As for the nomenclature, the following remarks may serve. The two younger epithets verna and autumnalis of Linné for androgyna and hermaphroditica of Juslenius are superfluous names and may as such be considered illegitimate.

When dividing *C. palustris* into two species, *C. androgyna* Juslen. and *C. hermaphroditica* Juslen., the name *C. palustris* L. must be conferred on one of the two species, according to the rules of nomenclature. According to those rules the name palustris would have to be used for the part comprising the type. As no herbarium material of *C. palustris* is known, and so no type can be pointed out, the name may be given to either species mentioned, at will. As the name *C. herma-*

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[1] By KOCH (1857) erroneously attributed to Kützing. In fact Kützing mentioned *C. verna*.

phroditica (*C. autumnalis*) has always been used for the species of the section Pseudo-callitriche, it is the best solution to replace *C. androgyna* Juslen. (*C. verna* L.) by *C. palustris* L., as was done by Druce (cf. Mansfeld, 1940).

Chapter VIII

DESCRIPTION OF THE SPECIES

In the species of the section Eu-callitriche we meet with a great number of modifications in the vegetative parts, especially in the size and shape of the leaves. Only *C. stagnalis* is more uniform under various conditions. The phenomenon of producing so many forms makes it impossible to give a description of a species including every form the species may develop. The numerous "formae" distinguished by several authors (Kützing a.o.) have no taxonomic value, whereas a division into varieties, which also has been tried, is not justified either, because of the fact that those varieties generally arise owing to the action of external conditions and thus do not rest on genetical factors.

In the following descriptions of the species therefore, we do not give but the theme; as to the variations be referred to Ch. III.

The descriptions have been made of plants in their optimal stage of development, that is to say with very well developed vegetative parts, flowering and fruiting abundantly.

Some remarks may follow.

The flowers are borne without any perianth in the axils of the foliage leaves. The male flower consists of one stamen, mostly provided with two transverse, falcate or more crescent-shaped membranaceous prophylla at its base.

The female flower consists of one pistil, mostly provided with two prophylla as well.

The male and female flowers of *C. obtusangula*, *C. platycarpa* and *C. hamulata* generally occur separately, rarely we meet with two flowers in one axil. In *C. stagnalis* and *C. palustris*, however, the latter situation is the most common. Here an anterior female flower and a posterior male one are borne in one leaf axil. Many authors considered both flowers to be parts of one hermaphrodite flower. This opinion is incorrect, for both, male and female flower are bearing their own two membranaceous prophylla.

As to the shape of the fruits we can say that in nearly all literature we meet with the opinion that the fruits of the species in the section Eu-callitriche—*C. obtusangula* excepted—are winged on the four angles. This, however, is not the case. The seeds, not the fruits, do possess a wing on their dorsal side or at their top. In this connection it may be emphasized that only Wahlenberg (1812) mentions winged seeds, in contrast with various other authors.

Near to the seedwings the walls of the fruits are thin and their cells are transparent. From this and in the side view one gets the impression that the fruits themselves are winged. In transverse section however (fig. 8) it is clear that such wings in reality are lacking. We can only say that the fruits are more or less keeled.

1. **C. hamulata** Ktzg. Plants from the village of Haren (prov. of Groningen)

a. *Waterform.* Plant generally winter annual, rooted in the mud. Stems branched, terete, — 40 cm. long, ca ¾ mm. thick. Young stems with pluricellular disc-shaped glands which are composed of about 12 to 18 radiate cells (fig. 7).

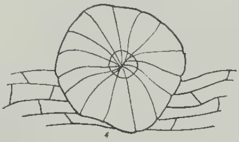

Fig. 7. C. hamulata. Gland of young stem. × 100.

Stem leaves opposite, linear, with a slightly widened and deeply emarginated apex (bicycle spanner), 1-nerved, green above, silvery greyish green beneath, 1-3 cm. long, ca 1 mm. broad. Floating rosettes tenuous, cup-shaped, composed of about 10 leaves (plate 7a). Lower leaves of the rosettes spathulate, about 1 cm. long; petiole light green, ca 1 mm. broad; lamina gradually tapering into the petiole, elliptical-obovate, with slightly emarginated apex, green above, greyish green beneath, with small disc-shaped glands on both sides, ca 6 mm. long, ca 3 mm. broad. Male and female flowers single in the axils of stem-leaves and lower rosette leaves, sessile, wholly submerged (plate 14a).

Prophylla—when present—small, narrowly falcate, membranaceous, white, to ½ mm. long.

Male flower: stamen small, at first erect, at time of pollination recurved towards one of the stigmata, ca 1 mm. long; filament white; anther reniform, rather colourless, ca ½ mm. broad. Pollen globular, colourless, without exine.

Female flower: stigmata thread-shaped, transverse, reflexed at base, turned backwards, colourless, at time of pollination from 1½ to 2 mm. long (plate 14a).

Fruit sessile, in side view nearly circular, ca 1¼ mm. across; basal rests of reflexed stigmata pressed close to the sides of the fruit. (Transverse section see fig. 8c).

Seed nearly bean-shaped, with narrow dorsal wing, darkbrown, 1 mm. long, ca ½ mm. broad (plate 16b).

Submerged pollination. Flowering time April-June. Common in ditches and brooklets on pleistocene sandy soils and dune soils (map 1, 2; p. 336).

b. Landform. Stems prostrate or ascendent, rooting at the nodes, branched, slender, bearing no rosette at the top, from 5 to 15 cm. long, ½ mm. thick. Leaves opposite, elliptical, ca 5 mm. long, 2 mm.

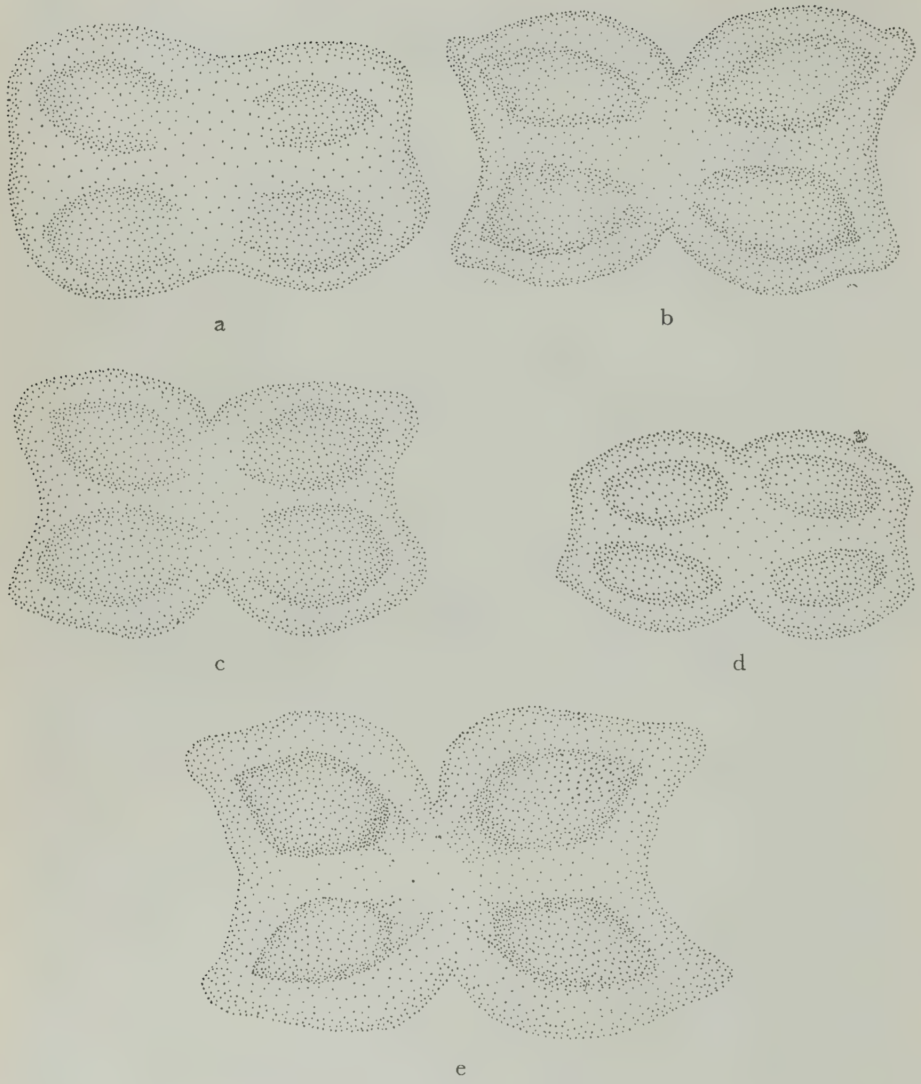

Fig. 8. Transverse sections of the fruits. × 27.
a. C. obtusangula, b. C. platycarpa, c. C. hamulata, d. C. palustris, e. C. stagnalis.

broad. Fruits sessile, sometimes stalked (plate 13a); stalks to ca 1 cm. long.

2 **C. obtusangula** Legall. Plants from the Island of Texel
a. Waterform. Plant perennial, rooted in the mud. Stems branched, terete, palish green, to 1½ mm. thick. Young stems glandulous. Glands irregularly disc-shaped, composed of about 8 radiate cells (fig. 9).

Stem leaves opposite, the lower ones of the main stems linear, emarginated at the apex, the upper elliptical or more or less rhomb-shaped.

Floating rosettes dense, composed of about 20 leaves, ca 2½ cm. across (plate 8a). Lower rosette leaves spathulate, thick, to 1½ cm. long; petiole markedly light coloured, to 7 mm. long, 1½ mm. broad; lamina rather abruptly tapering into the petiole, rhomb-shaped, somewhat emarginated at the apex, with small disc-shaped glands on both sides, green above, greyish green beneath, ca 8 mm. long, 6½ mm. broad; nerves 3-5, somewhat prominent above. Male and female flowers generally solitary, sessile, in the axils of rosette leaves only, each of them with 2 crescent-shaped prophylla at its base, partly raised above the water surface. After pollination the continued unfolding of the rosette brings the flowers down into the water.

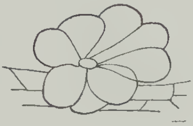

Fig. 9. C. obtusangula. Gland of young stem. × 100.

Male flower: stamen erect, ca 5 mm. long, after dehiscence recurvated and elongated; filament thread-shaped, white; anther reniform, yellow, to 1½ mm. broad. Pollen yellow, ellipsoidal, with well developed exine (fig. 10).

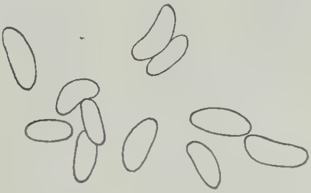

Fig. 10. C. obtusangula. Pollengrains. × 100.

Female flower (fig. 11c): stigmata 2, transverse, thread-shaped, divergent, at time of pollination ca 4 mm. long, after pollination nearly horizontally spread out, elongated. Fruit generally with erect short stigma rests, brown, in side view elliptical, longer than broad, 1½ mm. high, 1 mm. broad, in transverse section rounded rectangular (fig. 8a); median and lateral furrows very shallow.

Seed longly bean-shaped, unwinged, light brown, 1½ mm. long, ½ mm. broad (plate 16a). Air pollination. Flowering time May-autumn. In ditches and small streams near the coast (Haff-, Wadden-, Dune- and River district; map 3, 4; p. 340). Especially frequent in brackish water.

b. *Landform.* Stems prostrate or ascendent, rooting in the lower nodes, branched, generally bearing a rosette at the top, palish green, to ca 10 cm. long, 1 mm. thick. Young stems with disc-shaped glands. Stem leaves elliptical or narrowly rhomb-shaped. Rosettes composed of about 8 leaves. Rosette leaves more or less rhomb-shaped.

In 1953 we have grown *C. obtusangula* from the province of Zeeland (Netherlands). These plants were differing from the other *C. obtusangula*-specimens by their smaller, dark green rosettes and circular or obovate leaves with truncated apex (plate 8b).

For other differences cf. Ch. II and VI.

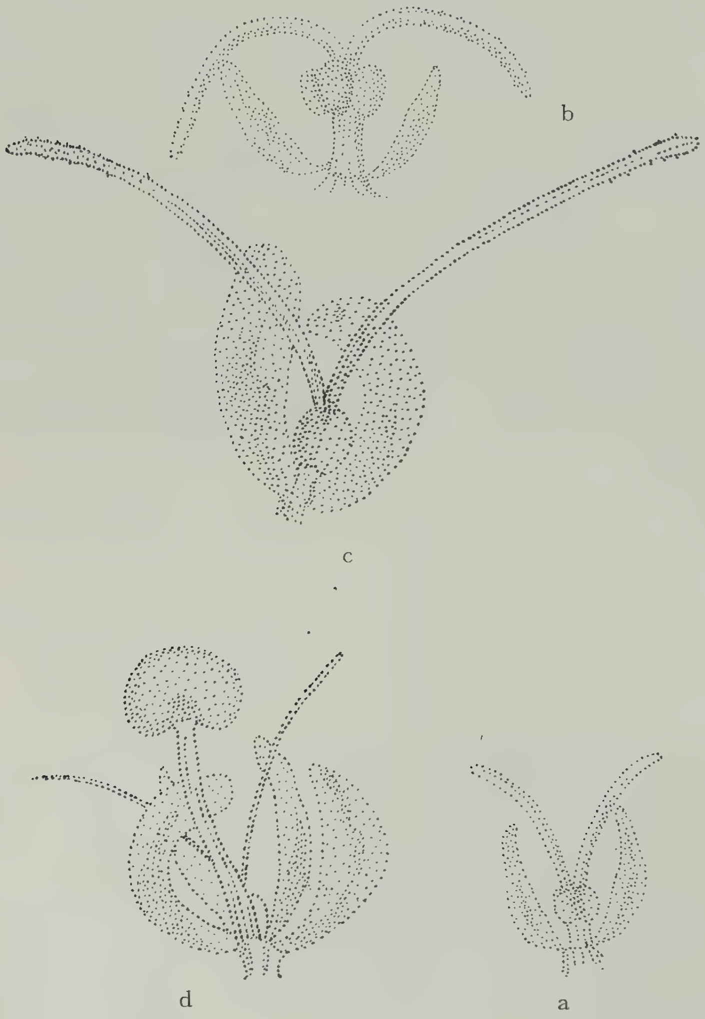

Fig. 11. Flowers. × 12½. a. C. stagnalis. Waterform. Young female flower. b. C. stagnalis. Waterform. Female flower at pollination time. c. C. obtusangula. Waterform. Female flower at pollination time, d. C. palustris. Well developed waterform. Male and female flower in one leafaxil, each of them with 2 prophylla.

3. **C. platycarpa** Ktzg. Plants from the village of Haren (prov. of Groningen)

a. *Waterform.* Plant perennial (generally about 2 years), rooted in the mud. Stems branched, terete, ca 3/4 mm. thick. Young stems glandulous. Glands irregularly disc-shaped, composed of about 8 radiate cells. Leaves opposite. Lower stem leaves generally linear or narrowly elliptical, emarginated at the apex. Floating rosettes composed of about 12 leaves (plate 7b). Lower rosette leaves spathulate, ca 1 1/2 cm. long; petiole ca 8 mm. long, to 1 1/2 mm. broad, light green; lamina more or less broad elliptical, more or less gradually tapering into the petiole, slightly emarginated at the apex, with small disc-shaped glands on both sides, green or glaucous, ca 1 cm. long, 7 mm. broad; nerves 3-5, somewhat prominent beneath.

Male and female flowers generally single, in the leaf axils of rosette leaves only, sessile, each of them with two crescent-shaped membranaceous prophylla, partly raised above the water surface, after pollination submerged.

Male flower: stamen ca 4 mm. long, with white thread-shaped filament, after dehiscence recurved and elongated; anther reniform, yellow, from 3/4 to 1 mm. broad. Pollen of various shape, globular, ellipsoidal, etc., yellow, with well developed exine (fig. 12).

Female flower: stigmata 2, transverse, thread-shaped, erect or patulous, 3-4 mm. long, after pollination widely spread out or somewhat recurved, elongated.

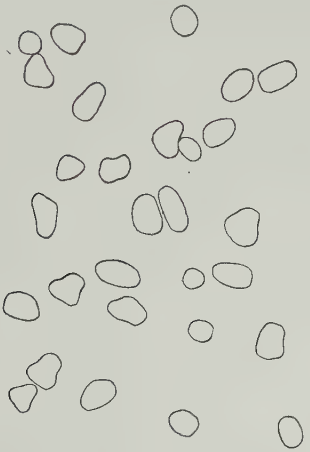

Fig. 12. C. platycarpa. Pollengrains. × 100.

Fruit sometimes with short, erect stigma-rests, carinated, in side view circular or shortly elliptical, from 1 1/2 to 1 3/4 mm. high, from 1 1/4 to 1 1/2 mm. broad; median furrows in transverse section (fig. 8b) crescent-shaped, lateral furrows rather deep. Seeds in a transverse section of the fruit never divergent, but parallel.

Seeds somewhat bean-shaped, with dorsal wing, brown, 1 3/4 mm. long, ca 3/4 mm. broad (plate 16c). Often 1-3 seeds do not develop.

Air pollination. Flowering time May-autumn. Common in ditches and brooklets. In fresh water (map 7, p. 345).

b. *Landform* (plate 13b)

Stems prostrate or ascendent, branched, with opposite, elliptical leaves. No well-marked rosettes. Prophylla small or lacking. Anthers generally smaller than those of the waterforms. Fruits commonly conspicuously keeled, light brown or brown. Seeds commonly with broader wings than those of the waterform, and more lightly coloured. Resembles in the vegetative parts sometimes *C. stagnalis* or *C. hamulata*.

4. **C. stagnalis** Scop. Plants from Schipborg (prov. of Drenthe)

a. *Waterform.* Plant annual or perennial.

Stems branched up to the top, rooting at many nodes, terete, to $^3/_4$ mm. thick, green. Young stems glandulous. Glands disc-shaped, composed of about 8 radiate cells. Stem leaves opposite, the lower ones elliptical or spathulate, slightly emarginated at the top, never linear. Floating rosettes composed of 6 to 8 opposite leaves (plate 9a). Lower rosette leaves spathulate, ca 15 mm. long; lamina broadly elliptical or circular, rather abruptly tapering into the petiole, very slightly emarginated at the top, generally 5-nerved, with small disc-shaped glands on both sides, bright green, ca 12 mm. long, ca 8 mm. broad.

Male and female flowers single or together in the leaf axils, each of them with two slightly crescent-shaped prophylla, partly raised above the water-surface, after pollination submerged.

Male flower: stamen erect, ca 2 mm. long, after dehiscence somewhat recurved and elongated; anther reniform, yellow, ca $1\frac{1}{2}$ mm. broad. Pollen globular, yellow, with exine (fig. 13).

Female flower stalked; stigmata two, transverse, thread-shaped, generally arcuate-recurved, ca 2 mm. long (fig. 11a, b). Fruit conspicuously keeled, light brown, in side view nearly circular, commonly somewhat broader than long, ca $1^3/_4$-2 mm. high, to 2 mm. broad; median furrows in transverse section deeply crescent-shaped, lateral furrows deep (fig. 8e).

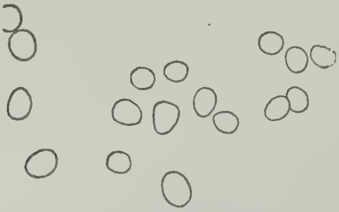

Fig. 13. C. stagnalis. Pollengrains. × 100.

Seeds in a transverse section of the fruit divergent (fig. 8e). Seeds broadly bean-shaped or somewhat reniform, broadly winged, light brown, from $1\frac{1}{2}$-$1^3/_4$ mm. long, $^3/_4$ mm. broad (plate 16e). Air pollination. Flowering time May-autumn. Estuaries, ditches and pools, in brook- and rivervalleys. In fresh and brackish water. Rare in the Wadden isles (map 9, p. 347).

b. *Landform.* Repent plants with branched stems, rooting at the nodes, with broadly elliptical or nearly circular leaves.

5. **C. palustris** L. Plants from Schipborg (prov. of Drenthe)
a. *Waterform.* Plant summer annual, with only a few roots. Stem unbranched or with some branches, terete, glabrous or with scattered disc-shaped glands near the top, to 25 cm. long, ca ¾ mm. thick. Glands composed of about 12-15 radiate cells (fig. 14). Stemleaves opposite, the lower ones mostly linear with emarginated apex, ca 3 cm. long, 1 mm. broad. Floating rosettes composed of ca 10 leaves, ca 1½ cm across (plate 9b). Lower rosette leaves spathulate, thin, 3-nerved, light green; lamina more or less gradually tapering into the petiole, broadly elliptical or nearly circular, ca 1 cm. long, ca 4 mm. broad.

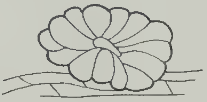

Fig. 14. C. palustris. Gland of young stem. × 100.

Male and female flowers commonly together in one leaf axil (fig. 11d), each of them with two rather straight membranaceous prophylla, partly raised above the water surface. Rarely one male flower and 2 female flowers in one leaf axil.

Male flower posterior; stamen rarely normally developed, generally more or less reduced, in well developed stage erect, ca 2 mm. long; anther small, yellow. Act of dehiscence often lacking.

Female flower sessile; stigmata erect-patulous, thread-shaped, in well developed condition ca 1½ mm. long, often more or less reduced, sometimes unequal in length.

Fruits small, narrowed in the lower half, in side view obovate, without stigma-rests, dark brown or blackish, 1 mm. long, at the top ¾ mm. broad; median and lateral furrows shallow. Seeds in a transverse section of the fruit slightly convergent (fig. 8d).

Seed narrowed towards the base, with small wing along the top, blackish, 1 mm. long, ⅓ mm. broad (plate 16d).

Apogamous, only in well developed conditions perhaps airpollination. Flowering time June-August. In "cowpuddles", in marshy brookvalleys. Rare (map 11, p. 348).

b. *Landform.* Small repent plants, glabrous or with a few disc-shaped glands. Leaves shortly linear or narrowly elliptical, to 4 mm. long, 2 mm. broad.

Male flowers rudimental, generally wholly disappeared (plate 14c). Stigmata of female flowers nearly entirely reduced (plate 14b).

KEY TO THE SPECIES

Only reliable for well developed, flowering and fruiting plants.

A. Waterforms

1*a*. Leaves all linear, with widened and deeply emarginated apex. Basal rests of the reflexed stigmata pressed close to the lateral sides of the fruit . . . . **C. hamulata**

b. Upper leaves spathulate, forming a well-marked floating rosette 2

2*a*. Rosette composed of about 20 rhomboid thick leaves. Fruit with rounded edges and very shallow median and lateral furrows, in side view elliptical, longer than broad. Seed unwinged. Pollen ellipsoidal . . . . **C. obtusangula**

Plants with almost circular leaves with truncated apex were found in the province of Zeeland.

b. Rosette composed of about 8-14 elliptical, circular or obovate leaves. Fruit more or less keeled. Seed winged 3

3*a*. Fruit small (1 mm. long), narrowed in the lower half, in side view obovate, blackish. Seed winged at the top . . . . **C. palustris**

b. Fruit larger, in side view circular or almost circular. Seed with dorsal wing 4

4*a*. Rosette cup-shaped. Stamens and stigmata wholly submerged. Anthers small, rather colourless. Pollen colourless. Stigmata reflexed at base. Basal rests of stigmata pressed close to the lateral sides of the fruit. . . . **C. hamulata**

b. Rosette more or less convex. Stamens and stigmata above the watersurface. Anthers yellow. Pollen yellow. Stigmata erect or recurved 5

5*a*. Rosette leaves generally elliptical. Pollen of various shape. Stigmata erect or spreading, to 5 mm. long. Seeds in transverse section of the fruit parallel . . **C. platycarpa**

b. Rosette leaves generally almost circular. Pollen globular. Stigmata generally arcuate-recurved, 2-3 mm. long. Seeds in transverse section of the fruit divergent . **C. stagnalis**

B. Landforms

1a. Pistil with very reduced stigmata. Stamen reduced, generally entirely lacking. Fruit small (1 mm.), narrowed in the lower half, in side view obovate, blackish. Seed winged at the top . . . . **C. palustris**

b. Pistil with well developed, thread-shaped stigmata. Fruit larger, in side view circular or elliptical 2

2*a*. Fruit with rounded edges and very shallow furrows, in side view elliptical, longer than broad. Seed unwinged. Pollen ellipsoidal. . . . . **C. obtusangula**

b. Fruit keeled. Seed with dorsal wing 3

3*a*. Stigmata reflexed at base. Rests of the stigmata pressed close to the lateral sides of the fruit. . . . **C. hamulata** *b*. Stigmata erect or recurved 4

4*a*. Stigmata erect - patulous. Seeds in transverse section of the fruit parallel. Leaves generally elliptical **C. platycarpa**

b. Stigmata arcuate - recurved. Seeds in transverse section of the fruit divergent. Leaves generally almost circular . . . . **C. stagnalis**

SUMMARY

For the study of the section Eu-callitriche in the Netherlands the cytological investigations formed the base for the outlines of the species. Owing to the chromosome sets, very different among themselves, the section might be split up into 5 fractions. This division proved to be consolidated as well by morphological, geographical and ecological characteristics and by the differences in the lifecycles. The combination of these characteristics at last led to a division into 5 species: *C. hamulata* Ktzg, *C. obtusangula* Legall, *C. platycarpa* Ktzg, *C. stagnalis* Scop. and *C. palustris* L.

While cultivating under various conditions we saw that—*C. stagnalis* excepted, being little variable—all species are very variable, especially in the vegetative parts. Many varieties, described in literature, must therefore be considered as modifications. Also *C. pedunculata* DC., described as a species, is probably a modification, and in that case belongs to *C. hamulata.*

Only a few varieties in ecological and morphological qualities are probably founded on hereditary factors (different leafshape and larger salt tolerance in *C. obtusangula* from the province of Zeeland, the brookform of *C. platycarpa*). For the time being no further systematic division was based on these characteristics.

In the species *C. obtusangula*, *C. stagnalis*, *C. palustris* and *C. platycarpa* plants occur with and without SAT-chromosomes. Between the two types of one species no further differences were observed, only in the case of *C. obtusangula* the existence of SAT-chromosomes proved to coincide with a differing leafshape and larger salt tolerance.

When studying the early stages in the mitosis, it became apparent that each satellite is composed of 2 parts, which unite before the metaphase into one (plate 4).

Most species show a clear preference for a certain environment, which also appears from the distribution regions.

In order to unravel the nomenclature, the knowledge of morphology, distribution etc. proved to be an aid. Thus e.g. *C. intermedia* Hoffm. must be rejected as a synonym for *C. hamulata* Ktzg, because of the quite different structure of flower.

A short survey of the principal data follows below.

C. hamulata Ktzg.

In several respects this species occupies a place of its own in the section. It deviates in the number of chromosomes ($2n = 38$; see plate 1) from the other species which have $2n = 10$ or $2n = 20$.

The chromosome set must be considered as the most asymmetrical; the lengths of the chromosomes are very different and as for the position of the centromeres, we find transitions from median to subterminal centromeres (fig. 1e). In contrast to the other species of the section no plants with SAT-chromosomes were observed.

Also in the structure of the flowers and in the submerged pollination *C. hamulata* differs from the other species (plate 14a; fig. 5). Because of its submerged pollination it is the only species able to fructify in deep water and in swiftly flowing water.

With regards to the distribution it is, for the Netherlands, typically a plant of sandy soils (pleistocene soils and dune soils, see map 1, 2; p. 336) where it grows in slightly acid - neutral water (cf. app. II, table I). *C. hamulata* is the only winterannual species.

By the fruit, with reflexed stigmata rests, laterally pressed close to it, it may easily be distinguished in any habit from other species.

C. obtusangula Legall has $2n = 10$ chromosomes (plate 3d). Some chromosomes belong to the longest of this section. The position of the centromeres is submedian - subterminal (fig. 1a). This salt tolerant species occurs in Europe in the mediterranean-atlantic coastal areas (map 5, p. 342). In the Netherlands we especially find it in oligohalinic-mesohalinic water of the wadden-, dune-, haff- and fluviatile districts (map 3, 4; p. 340). The water is neutral to slightly alcalic (cf. app. II, table II).

Well developed waterforms may be recognized by the dense rosette with rhombic, thick leaves (plate 8a), the fruit with rounded edges (fig. 8a), the non-winged seeds (plate 16a) and the ellipsoidal pollengrains (fig. 10). The species is a perennial.

A different form was found in the prov. of Zeeland. Those plants show an other leafshape (plate 8b), the seeds germinate in a higher salt concentration (cf. Ch. VI, table VI-X). The chromosome picture of these plants shows 2 SAT-chromosomes; the plants from Texel have no SAT-chromosomes. The satellite is connected to the small arm of the chromosome (plate 3e).

C. stagnalis Scop. also has $2n = 10$ chromosomes (plate 3a). But they are different in shape and size from those of *C. obtusangula.* All chromosomes have a subterminal centromere (fig. 1b). In this species plants were found with 0, 1 or 2 SAT-chromosomes (plate 3a, b, c). The satellite is connected to the long arm of the chromosome. The chromosome picture, observed by us, differs from that of the Russian plants of Sokolovskaja (1932); (cf. fig. 1*b*; fig. 3).

Just like *C. obtusangula C. stagnalis* is salttolerant (cf. Ch. VI, table XIV, XV) and occurs in coastal regions of Europe. However it also appears inland (map 10, p. 347). In the Netherlands (map 9, p. 347) we find it in the brookvalley areas and here and there along the coast (Biesbos). It is the only species that varies but little, and never forms linear leaves. The round rosette leaves (plate 9*a*), the globular pollen (fig. 13), the characters of the female flower (fig. 11a, b) and the broadly winged seeds (plate 16e) are characteristic for this species.

C. platycarpa Ktzg. The number of chromosomes is $2n = 20$ (plate 2a). All centromeres are subterminal (fig. 1c). Also in this species plants occur with 0 or 2 SAT-chromosomes (plate 2c, d; fig. 2). The satellite is connected to the long arm of the chromosome. *C. platycarpa* is an extremely variable species. In the Netherlands it proves to be the most common. It is much less restricted to special conditions of environment than the other species and occurs everywhere, except in brackish water (map 7, p. 345).

On account of its polymorphy and because it is often found in a sterile condition, this species often can be recognized as such after culture-experiments or cytological research only. That is probably the reason why it was not recognized thus far in our country.

C. palustris L., just like *C. platycarpa*, has $2n = 20$ chromosomes (plate 3f). They are smaller, however, and are nearly equal in size. (*C. palustris* has the smallest chromosomes of the 5 species of the section, fig. 1d).

Here we also find plants with 0 or 2 SAT-chromosomes (plate 3f, g). The satellite is connected to the small arm of the chromosome. For this species the connections between the metaphase-chromosomes in the mitosis are remarkable (plate 6a, b).

In habit *C. palustris* is the smallest of the 5 native Eu-callitriche species, the plants are tiny and little branched; as landform, the form in which it is mostly found, it is apogamous: the stigmata are abortive in these plants, while the stamens often have vanished altogether (plate 14b, c).

The embryosac probably develops from a somatic cell (plate 5).

The area of distribution is—so far as western Europe and Greenland are concerned—principally arctic-alpine (map 12, p. 349). In the intermediate regions it appears only rarely, and then only under very special environmental conditions ("cowpuddles"). Also in the Netherlands only few finding-places are known (map 11, p. 348). The species is a summerannual and well discernable by the very small dark fruit. The seeds are winged at the top only (plate 16d).

APPENDIX I

LOCALITIES OF THE FIVE SPECIES

1. *C. HAMULATA*

THE NETHERLANDS

Prov. of Drenthe: Koevorden 1859, h.L. 237, 251; Meppel, h.L. 91; Paterswolde 1855, h.G.; Peize, h.L. 39; Peize, h.G.; x Schipborg 1951; x Taarlo 1949; x Vosbergen, 1949; x Zuidlaren 1949, 1953.

Prov. of Friesland: Ameland (G 6. 51. 22) 1935, h.L. 112; Terschelling 1887, h.L. 139, 144, 537.

Prov. of Gelderland: Apeldoorn 1882, h.L. 926, 340-639; Apeldoorn 1892, h.L. 56; Cannenburgh near Vaassen 1874, h.L. 5; Cannenburgh near Vaassen 1885, h.L. 9; Harderwijk 1864, h.L. 130; Heelsum 1851, h.L. 335; Lent, h.L. 128; Loenen 1928, h.L. 937, 63-42; Malden 1924, h.K. & R.; Neerbos near Nijmegen 1865, h.L. 41, 42, 43, 44, 45, 47; Neerbos 1936, h.K. & R.; Neerbosser broek near Nijmegen, h.L. 6; Ooy 1938, h.K. & R.; Renkum, h.L. 336; Ruurlo 1882, h.L. 926, 340-580; Ruurlo 1886, h.L. 273; Ruurlo 1886, h.AMD 005005; Twello 1848, h.L. 101; Wolfheze, h.L. 394; x Wijchense ven 1949.

Prov. of Groningen: x Haren, Hortus ,,de Wolf" 1949-1951; Haren, Sassenhein 1951; x Haren Scharlakenhof 1949, 1951; Helpman, Groningen, h.L. 326; x Marum 1952.

Prov. of Limburg: x Arcen 1949, 1951.

Prov. of Noord-Brabant: Beugen (Q 6. 43. 32) 1933, h.L. 74; Berlicum, h.L. 77, 78; Boxmeer and Sambeek 1853, h.L. 81, 352; Boxmeer Zandbeek 1853, h.L. 81; Boxtelse heide 1847, h.L. 77, 80; Breda 1938, h.L. 935,5 - 58; Cromvoirt, h.L. 78; 's Hertogenbosch, h.L. 77, 78; Oeffelt, h.L. 73; Son 1850, h.L. 194, 203; Volkel (Q 5. 47. 41), h.L. 79.

Prov. of Noord-Holland: x Hippolytushoef 1953; x den Hoorn 1949; den Hoorn-den Burg 1921, h.GRO; x de Kooy 1949, 1951; Texel 1860, h.L. 276, 332; Texel 1895, h.L. 349.

Prov. of Overijsel: Delden 1870, h.L. 333; Denekamp, h.L. 246; Hardenberg 1892, h.L. 926, 340-611; Lattrop, Breklenkampse veld 1952, h.L. 95,372-711; Ootmarsum 1933, h.L. 393; Vollenhove 1898, h.L. 243.

Prov. of Utrecht: Beerschoten 1912, h.L. 942, 285-398; Blaauwkapel, h.L. 50, 231; de Bildt, h.L. 14, 15, 67; Eemnes 1895, h.L. 259; Rijzenburgse bos, h.L. 48, 49, 51, 52, 53, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 69, 264, 337, 345; Utrecht, h.L. 68, 265; Trajectum ad Rhenum (Utrecht), h.K.; Zeisterbos, h.L. 942, 285-134.

Prov. of Zuid-Holland: Endegeest, h.L. 355; Leiden 1820, h.B-B. 26; Loosduinen, h.L. 293.

OTHER COUNTRIES:

Belgium:

Casteau 1862, h.D.; Gedinne (Namur) 1866, h.L. 908, 281-381; 's Gravenwezel bij Antwerpen 1883, h.L. 908, 281-209.

Czechoslovakia:

Böhmerwald, h.D.

Denmark:

Bornholm: Olana 1850, h.C.; 1870, h.C.; 1876, h.C.

Jylland: Aalbaek 1872, h.C.; Blaavand 1899, h.C.; Blokhus 1888, h.C.; Esbjerg 1914 (distr. 27), h.C.; Fanö 1896, h.C.; Filsö 1950 (D 27), h.C.; Fyen, Fagsted mose 1926, h.C.; Holmslards Klut 1913, h.C.; Höve (Limfjord) 1864, h.C.; Höve 1868, h.C.; Hvidberg: Thy 1946 (D 7), h.C.; Lemvig 1874, h.C.; Mors 1901, h.C.; Ostbredden 1933 (D 52), h.C.; Römö, Kongsmark 1933, h.C.; Samsö 1890, h.C.; Samsö 1892, h.C.; Skjern 1932, h.C.; Skogens Nordstrand 1925, h.C.; Söndervig 1927, h.C.; Taasinge 1909, (D 32) h.C.; Torssö 1946, h.C.; Vinderup 1878, h.C.

Seeland: Furesöen Holte 1936, h.C.; Lac Dambusso près Copenhague 1866, h.L. 903, 364-1; Ravnsholt Hegn 1892, h.C.

Faroes:

Fuglö 1897, h.C.; Nolsö 1897, h.C.; Osterö, Göte, h.C.; Strömö 1897, h.C.; Syderö 1867, h.C; Syderö 1897, h.C.; Viderö 1897, h.C.

Finland:

Muonioalf (68°) 1915, h.K.

France:

Dep. Cantal: Auvergne Cantal, La Vigerie 1907, h.L. 911, 116-50.
Dep. Charente: Confolens 1879, h.Z. 65.
Dep. Eure-et-Loir: Dreux, h.D.
Dep. Haut-Rhin: Mulhouse 1851 h.D.; x Westhalten 1952.
Dep. Haute Saône: Champagney 1867, h.D.
Dep. Hérault: Gramont près Montpellier 1887, h.C.; Montpellier 1888, h.D.; Roquechanté 1896, h.Z. 66.
Dep. Indre-et-Loire: Landes de Bourgeuil 1873, h.Z. 70.
Dep. Loire: Montbrion 1887, h.D.
Dep. Loir-et-Cher: Romorantin 1862, h.D.
Dep. Maine-et-Loire: Angers, h.Z. 57.
Dep. Manche: Beaumont près Valognes 1861, h.L. 903, 364-34; 903, 364-35; 903, 364-36; h.D.; h.C.; h.B-B 29; Beaumont près Valognes, h.Z. 67; Cherbourg 1890, h.Z. 72; Tourneville 1891, h.D.; Valognes 1837, h.B-B 25; Valognes 1857, h.B-B 30; h.C.
Dep. Rhône: Charbonnière près Lyon 1852, h.D.
Dep. Seine-et-Marne: Fontainebleau 1829, h.D.; Fontainebleau, h.L. 903, 364-30; Fontainebleau, h.C.; h.D.; Fontainebleau 1853, h.Z. 229; Fontainebleau 1867, h.D.
Dep. Vosges: Epinal 1879, h.L. 909, 68-7; h.Z. 73; h.D.; Gérardmer 1849, h.D.; Huguemin, h.D.; Vogezen 1849, h.L. 903, 364-32.

Germany:

Bamberg 1905, h.D.; Bayreuth h.D.; Cleve 1871 h.Z. 68, 71; Cleve 1872, h.Z. 63; Coloniam (Köln), h.L. 903, 364-97; Flensburg 1878, h.D.; Freiburg 1900, h.Z. 60*a*; Hamm 1912, h.Z. 159; Hannover 1838, h.C.; Klein Wollmsdorf 1846, h.D.; h.Z. 4; Nürnberg 1856, h.L. 926, 156-488; Regnitz bei Bamberg 1904, h.C., h.B-B. 87, h.Z. 58, h.D.; Schleusingen, h.L. 910, 17-252; 910, 17-253; 910, 17-254; 910, 17-255; 910, 17-256; 910, 17-257; 910, 17-259; 910, 17-262; 910, 17-263; 910, 17-265; 910, 17-266; 910, 17-267; 910, 17-269. Schwarzwald, h.D., h.Z. 10; Tilleda 1878, h.Z. 64, h.D.; Waldmünchen, h.Z. 59; Wiesenthal 1863, h.Z. 52, 53.

Great Britain:

Clova, Angus, Scotl. 1935, v.c. 90, h.Ly.; W. Cornwall 1929, v.c. 1, h.Ly.; Dorset 1932, v.c. 9, h.Ly.; Farley 1926, v.c. 17, h.Ly.; Haroldwich, Shetland 1950, v.c. 112, h.Ly.; Isles of Scilly 1938, h.Ly.; Lancashire 1885, h.C.; Loch Ballates, S. Aberdeen 1934, v.c. 92, h.Ly.; Lyndhurst, Hants 1926, h.Ly.; Perthshire, Loch Acksay 1911, h.C.; Mid-Perthshire, Scotl. 1933, v.c. 88, h.Ly.; Scotland 1936, v.c. 105, h.Ly.; Sheffield 1944, v.c. 63, h.Ly.; Surrey 1945, v.c. 17, h.Ly.; Surrey, Mitcham Common, 1931, v.c. 17, h.Ly.; N. Wales 1931, v.c. 49, h.Ly.; Walton-on-Thames, h.Z. 56.

Greenland:

Amitsok 1883, h.C.; Amitsuarssuk 1937, h.C.; Arsukfjord (61° 15′ N) 1925, h.C.; Elv i Björnedal 1889, h.C.; Igalikofjord, h.C.; Julianehaab - Godthaab (60° 4′ - 64° 10′ N), h.C.; Nordkysten af Sargardsleg (68° 42′ N, 52° 30′ W) 1932, h.C.; Sukkertoppen 1884, h.C.; Tasermiutfjord (60° 16′ N) 1925, h.C.

Iceland:

Several localities: o.a. Hornafjord 1933, h.C. The other finding-places (h.C.) could not be located.

Italy:

Alpes bergamasques: Villasola, h.D.
W. Sicily: Ficuzza, Gurgo del Lupo 1856, h.Z. 46; h.D.; h.L. 903,364-115.

Spain:
Cerdagne, Llivia 1916, h.D.

Sweden:
Bohusia, Uddevalla in Ryån juxta Bräcke, h.C.; Längäsjö 1898, h.C.; Skåne: Eslöf 1885, h.K.; Svalöv 1928, h.D.; Småland 1849, h.C.; Upsala, h.L. 903, 364-13; Västmanland 1928, h.D.

Switzerland:
Canton Genève: Pinchat 1875, h.D.; Viry 1854, h.D.; Viry 1856, h.B-B 23; Bois de Viry 1860, h.B-B 5.
Canton Tessin: Lac majeur muralto 1903, h.D.
Canton Vaud: h.D.

2. *C. OBTUSANGULA*

THE NETHERLANDS

Prov. of Friesland: x Ameland (Buren) eendekooi 1952; Ameland (Nes), h.L. 233; Bolsward 1875, h.L. 909, 67-634; x Dokkum 1953; Leeuwarden, h.L. 921, 262-560.

Prov. of Gelderland: de Ooy, h.L. 251, 252.

Prov. of Groningen: x Delfzijl - Appingedam 1953; Hoogkerk h. Clas; x Rottum 1952; x Scheemda 1953.

Prov. of Limburg: Amby 1861, h.L. 329; Roermond (S 6. 54. 14), h.L. 399, 400.

Prov. of N. Brabant: Ulvenhouts Bos near Ginneken 1917, h.L. 928, 13-277.

Prov. of N. Holland: Alkmaar-Bergen 1878, h.L. 353; Diemerweg, h.L. 274; Haarlem 1877, h.L. 138; Haarlem, de Hout 1866, h.L. 226; Haarlem, de Hout 1871, h.L. 143; Hakkelaarsbrug near Naardermeer 1899, h.AMD 005004; Kraantje Lek 1872, h.L. 270; Naarden, h.L. 245; Schoten 1894, h.L. 933, 49–41; Schoten 1888, h.L. 347; Schoten 1870, h.L. 141; Sparendam 1888, h.L. 140; Texel 1895, h.L. 349, 350; x Texel, den Burg 1951; Texel, de Geul, (J 4. 52. 11) 1837, h.L. 940, 6–90; x Texel, de Cocksdorp, 1949, 1951, 1952, 1953; x Texel, den Hoorn 1949; x Texel, de Muy 1949, 1951; x Texel, Oosterend 1951; x Texel, Prins Hendrik Polder 1951; x Texel, Pijpersdijk 1949, 1951, 1952, 1953; Schelvisnol 1933, h. GRO; x Vogelenzang near Haarlem 1953; Wieringen 1856, h.L. 274.

Prov. of Overijsel: Kampen h.L. 326; Zwolle (L 6. 54. 44), h.L. 926, 340-597; Zwolle 1913, h.L. 40.

Prov. of Utrecht: Leersum 1919, h.L. 921, 61-148.

Prov. of Zeeland: Domburg, Duinvliet, 1877, h.L. 376; Domburg Oranjezon, 1839, h.L.; x Goes 1953; Haamstede 1844, h.L. 372; x Kapelle-Biezelinge 1953; Kapelle, h.L. 82, 328; Kapelle 1898, h.L. 398; Kloetinge, h.L. 88; Kloetinge 1886, h.L. 103; Kloetinge 1886, (R 2. 37. 2), h.L. 926, 340–612; x Kloetinge 1953; Kloosterzanden 1845, h.L. 371; Nieuwvliet 1877, h.L. 937, 351–362; Passegeule 1861, h.L. 237; id. bij Biervliet, h.L. 318; Tholen 1877, h.L. 86, 87; Walcheren, h.L. 236; Zuid-Beveland, h.L. 324; Zuid-Beveland 1839, h.L. 369; Zuid-Beveland 1840, h.L. 209; Zuid-Beveland 1840, h.L. 358; Zuid-Beveland 1843, h.L. 130.

Prov. of Z. Holland: Barendrecht 1939, h.L. 953, 178-351; x Biesbos 1953; Eindmeer (Rozenburg), h.L. 272; Hoek v. Holland 1879, h.L. 359; Hoek v. Holland 1900, h.L. 910, 286–704; Katwijk, h.L. 155; Katwijk 1894, h.L. 933, 49–39; Katwijk-Noordwijk 1897, h.L. 300, 301, 302; Katwijk, Leidse duinwater Mij 1952, h.L. 95, 372–330; Leiden, h.L. 356; Leiden 1847, h.L. 150; Leiden, Leidse vaart, 1867, h.L. 228; Lisse 1894, h.L. 933, 49–39; Noordwijk 1872, h.L. 147; Noordwijk 1891, h.L. 928, 13–276; Noordwijk-Voorhout 1939, h.L. 945, 256–232; Noordwijk 1939, h.L. 953, 178–354; Schiedam 1892, h.L. 228; Valkenburg, h.L. 187; Wassenaar 1897, h.L. 298; Zoeterwoudse weg, h.L. 23.

OTHER COUNTRIES:

France:
Dep. Alpes maritimes: Entre Juan-les-Pins et le Golfe Jouan 1912, h.Z. 160.
Dep. Charente-Inférieure: Saint Georges d'Oléron 1892, h.D.; Saint Georges d'Oléron 1892, h.B-B 37; id. 1890, h.B-B 34.
Dep. Eur-et-Loir: Dreux 1843, h.D.
Dep. Gironde: La Teste 1897, h.D.
Dep. Hérault: Montpellier 1881, h.C.; Montpellier 1851, h.Z. 118.
Dep. Manche: Yvetot près Valognes 1857, h.K.; Yvetot près Valognes 1857, h.B-B 36.
Dep. Orne: Flers 1890, h.D.
Dep. Sarthe: Le Mans 1897, h.D.
Dep. Vendée: Ile d'Elle, h.D.; Ile d'Elle 1883, h.C.; Luçon 1868, h.D.; Luçon 1903, h.D.; Vendée 1853, h.L. 903, 364–44.
Corsica: Ajaccio 1913, h.Z. 131, 132.

Great Britain:
Dorset 1928, v.c. 9, h.Ly.; Essex: Tilbury 1885, h.C.; Isles of Scilly 1940, no. 402, 409, h.Ly.; W. Kent 1923, 1943, v.c. 16, h.Ly.; Norfolk: Acle 1883, h.C.; h.Z. 88; Caiston-Yarmouth 1884, h.C.; Somerset 1930, 1931, v.c. 6, h.Ly.; E. Sussex: Broomhill 1932, v.c. 14, h.Ly.; E. Sussex: Iford 1931, v.c. 14, h.Ly.

Italy:
Napoli, h.L. 903, 364-93; Neapel h.C.; Pistoia 1886, h.B-B 58.
Sardiny: Orune, iter Sardoum 1899, h.D.
Sicily: Palermo 1841, h.D.; Palermo 1850, h.D.

North Africa:
Algiers: Algér, h.D.; Algers 1870, h.C.; Constantine 1888, h.D.; Constantine 1915, h.D.; Dj. Ouach près Constantine 1889, h.D.
Tunis: Aïn-Draham 1909, h.D.

Switzerland:
Canton Genève: Compesière 1848, h.D.; Etrambières 1872, h.B-B 45, 48; Genève 1793, h.D.; Puplinge 1879, h.D.; Puplinge 1880, h.D.; Roëllebot 1854, h.D.; Veyrier 1875, h.D.; Veyrier 1880, h.D.
Canton Valais: Valais 1771, h.D.

3. *C. PLATYCARPA*

THE NETHERLANDS

Prov. of Drenthe: x Anlo 1951; Meppel (K 6. 76. 21) 1930, h.L. 114; Peize, h.L. 128; x Ruiner Aa 1952.

Prov. of Friesland: x Bakkeveen 1953; x Kollum 1953; Oldeberkoop, h.L. 224.

Prov. of Gelderland: Apeldoorn 1883, h.L. 125, 378; Bennekom 1890, h.L. 93; Bennekom 1902, h.L. 928, 7–58; x Corle 1951; x Eibergen-Borculo 1951; Hees near Nijmegen 1851, h.L. 103, 218, 256; x Korenburgerveen 1951; Lent near Nijmegen, h.L. 219; x Lichtenvoorde 1951; Nijmegen, h.L. 247; Putten 1931, h.L. 388; x Ratum 1951; Ubbergen 1928, h.K. & R.; x Winterswijk 1951.

Prov. of Groningen: Dorkwerd, h.L. 232; Dorkwerd 1855, h.GRO; Groningen 1856, h.L. 116; h.GRO; x Haren 1951, 1952, 1953; x Leens 1951; x Marum 1952.

Prov. of Limburg: x Arcen 1949, 1951; Bunde 1904, h.L. 375; Eijsden near Oude Maas 1894, h.L. 215, 311; Eijserbos h.L. 954, 062-591; x Heerlen-Brunssum 1951; Mook (Q 6. 23. 33) 1938, h.L. 107; Plasmolen (Q 6. 23. 44) 1919, h.L. 923, 123-345; Plasmolen (Q 6. 23. 43) 1933, h.L. 106; Ottersum 1897, h.L. 214; x Kasteel Wittem 1951; x Wijlre-Mechelen 1951.

Prov. of Noord-Brabant: Bergen op Zoom, h.L. 196; Bergummerheide 1864, h.L. 909, 67 -630; 's Hertogenbosch, h.L. 196; Loon op Zand 1939, h.L. 942, 123-348.

Prov. of Noord-Holland: Alkmaar-Bergen 1878, h.L. 353; Haarlem, de Hout, h.L. 910, 283-633; Heemstede, h.L. 269; Naarden 1901, h.L. 279; Schoten 1894, h.L. 928, 13–261; Vogelenzang 1867, h.G.; Vogelenzang 1875, h.G.

Prov. of Overijsel: x Diepenheim-Goor 1951; Hardenberg 1892, h.L. 926, 340–627; h.L.926, 340–626; Ittersum near Zwolle 1894, h.L. 240; Ittersum near Zwolle (L 6. 65. 43) 1894, h.L. 926, 340–55; Tubbergen-Reutum 1935, h.L. 389.

Prov. of Utrecht: Amersfoort 1906, h.L. 928, 7-13; de Bilt 1930, h.L. 391; Bunnik 1912, h.L. 947, 334-312; Soesterveen 1925, h.L. 258.

Prov. of Zuid-Holland: Delfshaven near Rotterdam 1909, h.L. 934, 83-170; Dordrecht 1849, h.L. 317; Dubbeldam, h.L. 280; Dubbeldam 1848, h.L. 317; den Haag (N 3. 55. 24), h.L. 158; den Haag, Clingendaalse weg 1900, h.L. 354; den Haag 1933, h.L. 951, 159–124; Leiden, h.L. 356; Leiden 1847, h.L. 150; Leiden 1901, h.L. 315; Noordwijk, h.L. 98, 99; Noordwijk 1849, h.L. 101, 357; Noordwijk 1913, h.L. 928, 13–262; Rotterdam h.L. 292; Rotterdam 1850, h.L. 297; Rotterdam 1918, h.L. 923, 134–80; Rotterdam 1933, h.L. 934, 59–66; Rijnsburg 1845, h.L. 96; Rijnsburg, h.L. 338, 339, 340, 341, 342, 343, 344; Warmond 1841, h.L. 151; Zoeterwoudse weg, h.L. 23.

OTHER COUNTRIES:

Austria:
Austria superior: Aistersheim, h.L. 915, 150-252; Mannersdorf 1890, h.Z. 99.

Belgium:
x Lixhe 1949.

Czechoslovakia:
Prope Gratzen 1894, h.D.; h.Z. 102; Gratzen, h.D.; h.Z. 98; Wiesenbach bei Sonntag in Südböhmen 1884, h.Z. 101.

Denmark:
Jylland: Fur 1917, h.C.; Guden Aa ved Randers 1899, h.C.; Lustrup ved Ribe 1886, h.C.; Ribe 1887, h.C.; Tradsborg Baek 1886, h.C.
Seeland: Arrenaes (D 45) 1936, h.C.; Dyrehavn (D 45) 1867, h.C.; Hillerød E. of Store Lake Gribsø (D 45) 1946, h.C.; Hornbaek 1894, h.L. 950, 142-238; Lyngby in Dyrehavn (D 45) 1946, h.C.; Sondersoën 1885, h.C.; Töllöse (D 44) 1890, h.C.

Finland:
Prope Helsingfors 1884, h.Z. 106.

Germany:
Bamberg 1905, h.D.; Berlin 1895, h.Z. 94, 104, 187; Bremen 1894, h.Z. 103; Breslau 1872, h.D.; Eberswalde 1878, h.D.; Regnitzaltung Bamberg 1905, h.D.; Schleusingen, h.L. 910, 17-270; h.L. 910, 17-272; h.L. 910, 17-273; h.L. 910, 17-274; h.L. 910, 17-275; h.L. 910, 17-276; h.L. 910, 17-278; h.L. 910, 17-279; h.L. 910, 17-280; h.L. 910, 17-281; h.L. 910, 17-282; h.L. 910, 17-284; h.L. 910, 17-291; h.L. 910, 17-292; h.L. 910, 17-293.

Jugo-Slavia:
Bosnië 1848, h.D.

Roumania:
Transsilvanië, Retteg 1862, h.D.; Transsilvanië 1875, h.D.

Sweden:
Skåne: Bl. Lösen 1888, h.C.; Christianstad 1881, h.Z. 107; h.D.; Freuningen 1899, h.C.; Göteborg 1898, h.C.; Södermanland, par. Strängnäs, Eldsund 1924, h.D.

Switzerland:
Canton Valais: Col de Morgins 1868, h.D.; Lac du Golset près Morgins 1918, h.D.
Canton Vaud: Marais de la Dôle, h.D.

West Russia:
Lwow, h.Z. 105.

4. *C. STAGNALIS*

THE NETHERLANDS

Prov. of Drenthe: Havelte 1937, h.L. 953, 178-379; Lheeërzand 1948, h.AMD. 008604; Koevorden 1859, h.L. 237; x Roden-Lieveren 1951; x Schipborg 1949, 1950, 1951, 1952, 1953.

Prov. of Friesland: Terschelling, Midsland 1939, h.L. 953, 178–350; Terschelling 1950, h.K. & R.

Prov. of Gelderland: Epe 1890, h.L. 124 or 127; Groesbeek 1925, h.K. & R.; Groesbeek (Q 6. 23. 21) 1933, h.L. 123; Montferland near 's Heerenberg 1866, h.L. 230; Nijmegen, h.L. 247; Renkum 1897, h.L. 124; Ruurlo, h.L. 126; Wildenborgh 1833, h.L. 204.

Prov. of Noord-Brabant: Boxmeer 1853, h.L. 199, 205, 352; Breda-Terheyden 1916, h.L. 953, 222-960; Liesbos h.L. 188; Rozendaal 1860, h.L. 367; Tilburg 1940, h.L. 953, 222-929; Vliet, Moerdijk 1860, h.L. 367.

Prov. of Overijsel: de Lutte 1948, h.L. 948, 313-439.

Prov. of Utrecht: Utrecht, Ezelsdijk, h.L. 942, 285-404; Utrecht, h.L. 134; Vreeswijk, h.L. 135.

Prov. of Zuid-Holland: x Biesbos 1952; Dordrecht, Polder Jager 1838, h.L. 165; Dordrecht, Noordendijk 1850, h.L. 170, 202; Dordrecht, Noordendijk, h.L. 165; Leiden, h.L. 129; Moerdijkbrug 1938, h.L. 935, 5–56; Rotterdam, bij Nieuwe Maas 1908, h.GRO.

OTHER COUNTRIES:

Denmark:
Jylland: Astrap 1902, h.C.; Fanö 1880, h.C.; Fanö 1896, (Dist. 27) h.C.; Fanö 1899, h.C.; Fenshold, Stovskov 1913, h.C.; Filsö, (D. 27) 1950, h.C.; Heerup i Thy 1925, h.C.; Hirtshals 1898, h.C.; Hostrup sø ved Aabenraa 1934, h.C.; Colding Kirkeskov paa Vej 1927, h.C.; Kongshuvet 1913, h.C.; Lilleballe Skov ved Kolding, (D. 25) 1927, h.C.; Lustrup v. Ribe 1886, h.C; Moselud ved Teylgaards-vest, Viborg 1904, h.C.; Skibild 1872, h.C.; Silkeborg 1867, h.C.; Sondervig ved Ringkobing 1893, h.C.; Sondervig 1926, h.C.; Stogholmsö 1906, h.C.; Varde, Gröster ved Oxby 1899, h.C.; Varde, Trisvang 1950, (B.T.U. distr. 27) h.C.
Seeland: Mose ved Türesöen 1935, h.C.; Vallenzbaek Mose 1932, h.C.; Ved Rörvig 1899, h.C.

Faroes:
Kunö 1897, h.C.; Nolsö 1897, h.C.; Strömö, h.C.; Strömö, Thorshavn 1867, h.C.; Strömö, 1867, h.C.; Suderö 1897, h.C.; Viderö, Ostrig 1897, h.C.; Viderö, Krannasund 1897, h.C.

France:

Dep. Charente-Inférieure: La Matière-en-Oléron 1890, h.B-B 78; La Matière-en-Oléron 1892, h.D.; h.B-B 79.

Dep. Eur-et-Loir: Dreux, h.D.

Dep. Gironde: Arlac près Bordeaux 1842, h.D.; De la route de Casaux 1897, h.D.

Dep. Haute Garonne: Toulouse 1857, h.D.

Dep. Haute Savoie: Alpes d'Annecy (nr 4-9), h.B-B 88; Collet des Glisses, h.B-B 101.

Dep. Loire inférieure: Nantes 1829, h.D.

Dep. Manche: Herbeville près de Valognes 1863, h.L. 903, 364-49; h.C.; h.D.; Herbeville 1863, h.L. 903, 364-50.

Dep. Rhône: Arnas 1877, h.D.; h.L. 903, 364–45; h.L. 381; Arnas 1898, h.C.

Dep. Seine: Paris, h.D.

Dep. Seine-et-Marne: Fontainebleau, h.B-B 68, 83.

Dep. Somme: Le Eréport dans le Bresle 1892, h.D.

Dep. Vendée: Ile d'Elle 1898, h.C.

Dep. Vosges: Epinal, h.D.

Corsica:

Ajaccio 1849, h.D.; Bastia 1881, h.B-B 76.

Germany:

Bayreuth 1876, h.Z. 141; Borkum 1871, h.Z. 143, 144; Bremen, h.Z. 137; Cleve 1871, h.Z. 134; Cleve 1872, h.D.; Dresden, h.L. 903, 364–55; Immelborn 1876, h.Z. 140; Immelborn 1877, h.Z. 139; Immelborn 1879, h.Z. 138; h.D.; h.L. 944, 202–202; Schleusingen, h.L. 910, 17–283; 910, 17–285; 910, 17–286; 910, 17–290; Tiefendorf bei Annen 1874, h.Z. 150; Im Bache bei Dolgemost, Putbus 1855, h.L. 903, 364–60.

Great Britain:

Cumberland: Ardale 1911, h.C.; Isles of Scilly 1940, h.Ly.; Perthshire: Trossachs, Loch Ackray 1911, h.C.; Somersetshire: h.K.; Staffordshire: Kuypersley 1885, h.C.; E. Sussex 1936, v.c. 14, h.Ly.; Surrey: Ashstead 1894, h.D.; E. Sutherland: Loch Fleet 1936, v.c. 107, h.Ly.

Iceland:

Reykir (S. Isl.) 1911, h.C.; Reykir 1934, h.C.; Reykjafors 1911 (S. Isl.), h.C.; Reykjavik 1876, h.K.; Ved Reykjavik 1884, h.K.; Reykjavik 1888, h.C.; Skribla 1876, h.C.; Vik (S. Isl.) 1933, h.C.

Italy:

Colico (Alpes bergamasques) 1912, h.D.; Padova, h.Z. 136; Venetië 1897, h.C.
Sicily: Caronia, h.Z. 145; Messina 1856, h.D.

Norway:

Nordre Throndhjemsamt, h.C.; Tilder Lerfossen 1926, h.C.; Ulvik 1904, h.B-B 63.

Portugal:

Coimbra, Baleia, h.Z. 126; Coimbra, Porto dos Bentos 1904, h.C.; x Coimbra 1949, 1952, 1953 (bot.garden); Douro litoral, Espinho Beira de ribeiro 1946, h.L. 950, 101-780; Terra de Nagueira 1909, h.D.

Spain:

Cerdagnes, Ur, 1927, h.D.; Guipuzcoa, Pasajes 1895, h.C.; Jerez 1883, h.C.; Merquita (Minorca, Baléaren) 1873, h.Z. 148.

Sweden:

Prov. Dalarna, par. Folkärna, prope Västansjö 1928, h.D.; Kronob(erg?) 1867, h.C.; Smaaland, Femsjö, h.C.; Smaaland, Langasjö 1897, h.C.; Smaaland, Langasjö 1898, h.C.; ved Nedsjön 1926, h.C.; Smaaland 1898, h.C.; Västergotland, Göteborg 1927, h.D.

Switzerland:

Canton Aargau: Frauenwald bei Rheinfelden, 1852, h.D.

Canton Genève: Bois de Viry 1840, h.B-B 63; Ecogia près Versoix, h.D.; Lancy Onex 1877, h.D.
Canton Tessin: Lac majeur, Muralto, h.D.; Lac de Muzzano, h.D.

5. *C. PALUSTRIS*

THE NETHERLANDS

Prov. of Drenthe: Koevorden 1859, h.L. 251; Koevorden 1859, h.L. 234.

Prov. of Gelderland: Hees near Nijmegen, h.L. 256; Nijmegen, h.L. 248, 249; Persinge, h.L. 250.

Prov. of Noord-Brabant: Berlicum 1847, h.L. 76, 191, 194, 195, 291, 317; 's Hertogenbosch 1847, h.L. 117, 169, 196; 's Hertogenbosch 1891, h.L. 941, 314–812.

Prov. of Zuid-Holland: Heikop near Vianen, h.L. 283; Vianen, h.L. 282.

OTHER COUNTRIES:

Austria:
Kreuzberg (Tirolia austr. orient) 1875, h.D.; Linz 1849, h.Z. 165; Salzburg 1904, h.Z. 186.

Denmark:
Hornbaek (Seeland) 1922, h.C.; Mariager (Jylland) 1942, h.C.; N. Jylland 1950, h.C.; Petersborg 1846, h.C.; Rostgaardsdam 1862, h.C.; Stensvod Mose (Seeland), h.C.; Tröbjerg 1913, h.C.; Tversted aa 1901, h.C.

England:
Petersham (Surrey) 1877, h.D.

Estonia:
Wormsi 1926, h.C.

Finland:
Maikoniemenjoki, Savonia borealis 1911, h.C.; Rovaniemi (66° 40′) 1930, h.C.

France:
Dep. Eur-et-Loir: Dreux, h.D.
Dep. Isère: Grenoble 1848, h.D.
Dep. Haute Savoie: Alpes d'Annecy 1909, h.B–B 84; Alpes d'Annecy 1912, h.B-B 84; Beaufort 1847, h.D.; Collet des Glisses 1900, h.B-B 101; Au dessus de Conflans 1897, or 1899, h.D.
Dep. Savoie: Albertville 1862, h.D.; Mont Cenis 1867, h.Z. 184; Mont Cenis 1894 (?), h.B-B 94; Sommet du Cormet 1861, h.D.; Lac de la Girottaz 1862, h.D.; Hauteluce 1861, h.D.; Au M^{e} Mirantin 1861, h.D.

Corsica:
Lago di nino 1932, h.Z. 164.

Germany:
Baden 1893, h.Z. 179; Hollingsted (Syd-Slesvig), h.C.; Schleusingen, h.L. 910, 17-287; h.L. 910, 17-289; Schwarzwald, h.Z. 178; Wittenburg 1849, h.Z. 180.

Greenland:
Cape Hedlund (72° 10′, 26° 10′) 1932, h.C.; Holstenborg 1886, h.C.; Igaliko 1828, h.C.; Igaliko 1888, h.C.; Jakobshavn 1892, h.C.; Jacobshavn 1891, h.C.; Kehestat (71°), h.C.; Kung Oskarshavn 1883, h.C.

Iceland: several localities, a.o.:
Breidamerkursandi (Syd Isl.) 1908, h.C.; Flateyr (N. Isl.) 1891, h.C.; Geysir (S.W. Isl.) h.C.; "Hraun i Fljotum" 1899, h.C.; "Hraun" (N. Isl.) 1899, h.C.; Langarvatn (S. Isl.) 1907, h.C.; Langarvatn 1911, h.C.; Myvatn 1928,

h.C.; Reykjalang i Olafsfirdi, h.C.; Reykjalang 1890, h.C.; Skagafjörd 1930, h.C.

Italy:
Alpes bergamasques 1912, h.D.; Bormio 1911, h.Z. 176, 177; Piémont 1880, h.Z. 181.

Norway:
Finmarken 1838, h.C.; Larvik, h.C.; Oystre Slidre, Kvithøvd 1930, h.C.; Rendalen ved Hornset 1899, h.C.

Poland:
Peilau 1887, h.Z. 172.

Sweden:
Gothenburg, h.C.; Lexssand (Dalarna) 1849, h.C.; Mälaren (Södermanland) 1924, h.D.

Switzerland:
Canton Genève: Alpes Léman., Mont de Granges 1920, h.D.; Alpes Léman., Plateau d'Avoria 1920, h.D.; Alpes Léman., Crète de Chaufleurie 1920, h.D.; Bois de Viry 1840, h.B-B 63.
Canton Graubunden: Lago di Lagalb 1905, h.D.; Lenzerheide, Crap la Pala, 1922, h.D.
Canton Tessin: Val Bavona 1904, h.D.; Frasco 1903, h.D.; Locarno 1900, h.D.; Prumogna 1905, h.D.
Canton Valais: Foret d'Aletsch 1934, h.D.; Vallée de Binn 1887, h.D.; Alpe de Louvie sur Fionnay 1917, h.D.; Près le Lancet 1900, h.B-B 84; Münster (Magordi), h.D.; Bourg. St. Pierre (route du Grand St. Bernard) 1919, h.B-B 85; Mares au glacier de Rhône 1895, h.D.; Sur le Simplon 1822, h.D.
Canton Vaud: Bex, h.B-B 80, 81; Alpes de Bex, h.B-B 90.

APPENDIX II

QUALITIES OF WATER IN DUTCH LOCALITIES

TABLE I
C. hamulata

Locality	pH	Content of Cl′ in mgr/L
Arcen (prov. of Limburg) . . . . . . .running water	6.0	32
Marum (prov. of Groningen) . . . . .stagnant water	7.2	96
Bot. Garden „de Wolf”. . . . . ”	7.2	36
Sassenhein (prov. of Groningen) . .running water	6.2	67.5
Scharlakenhof ” . . ”	5.8	trace
” ” . . ”	6.1	trace
Schipborg (prov. of Drenthe) . . . . . ”	6.2	67
Hippolytushoef (prov. of N.-Holland). .stagnant water	6.7	852
“Oude Kamp” (Texel) . . . . .cattlepond	6.7	128
de Koog ” . . . . ”	6.5	39
den Hoorn ” . . . . .running water	7.7	64
de Dennen ” . . . . ”	6.6	112
den Hoorn ” . . . . ”	7.2	34
” ” . . . . ”	6.6	50
Ameland . . . . ”	7.1	71

TABLE II. *C. obtusangula*

	Locality		pH	Content of Cl′ in mgr/L
1	Rottum (prov. of Groningen)	running water	9.0	1161
2	,, ,,	,,	7.4	622
3	,, ,,	,,	8.1	1995
4	,, ,,	,,	8.0	1960
5	Dokkum (prov. of Friesland)	stagnant water	7.2	114
6	Vuurtoren (Texel)	running water	8.0	710
7	,, ,,	,,	7.8	1406
8	,, ,,	,,	8.2	704
9	Bouwlust ,,	,,	7.0	315
10	,, ,,	,,	7.0	152
11	,, ,,	,,	7.1	185
12	Duinweg Cocksdorp (Texel)	,,	7.6	96
13	Muysloot (Texel)	,,	7.6	604
14	,, ,,	,,	7.8	614
15	Museum ,,	,,	6.8	131
16	Cocksdorp ,,	,,	7.8	220
17	Prins Hendrik polder (Texel)	,,	7.8	554
18	den Hoorn (Texel)	,,	7.7	51
19	,, ,,	,,	7.7	90.5
20	,, ,,	cattle pond	6.7	128
21	Oosterend ,,	running water	6.5	390
22	Oude Schild ,,	,,	6.5	312
23	,, ,,	,,	6.5	213
	Cultures botanical garden “de Wolf”			
	experimental brook (layer of ashes)		7.8	21
	,, ,,		7.9	25

TABLE III. *C. platycarpa*

Locality		pH	Content of Cl′ in mgr/L
Marum (prov. of Groningen)	stagnant water	7.2	96
Wehe ,,		8.6	32
,, ,,	stagnant water	7.0	130
Botanical Garden “de Wolf”	,,	7.8	27
,,	running water	7.8	21
,,	stagnant water	7.6	29
Scharlakenhof (prov. of Groningen)	running water	6.1	trace
Dokkum (prov. of Friesland)	stagnant water	7.2	114
den Hoorn (Texel)	cattle pond	6.7	128
Oude Schild (Texel)	running water	6.5	312
,, ,,	,,	6.5	213
Goor (prov. of Overijsel)	,,	7.4	43
Corle (prov. of Gelderland)	,,	7.0	27
Winterswijk (prov. of Gelderland)	stagnant water	6.8	46
Arcen (prov. of Limburg)	running water	6.0	32
Kasteel Wittem (prov. of Limburg)	stagnant water	7.0	12
Mechelen (prov. of Limburg)	running water	7.5	14
Brunssum ,,	,,	6.6	trace
Cultures botanical garden ,,de Wolf”			
“cowpuddles”		7.9	35.5
experimental brook meadow		7.8	21
,, arboretum		7.8	27

TABLE IV
C. palustris

Locality	pH	Content of Cl′ in mgr/L
"Cowpuddles" brookvalley Schipborg (prov. of Drenthe)	6.2	67
"Cowpuddles" bot. garden "de Wolf"	7.9	35.5

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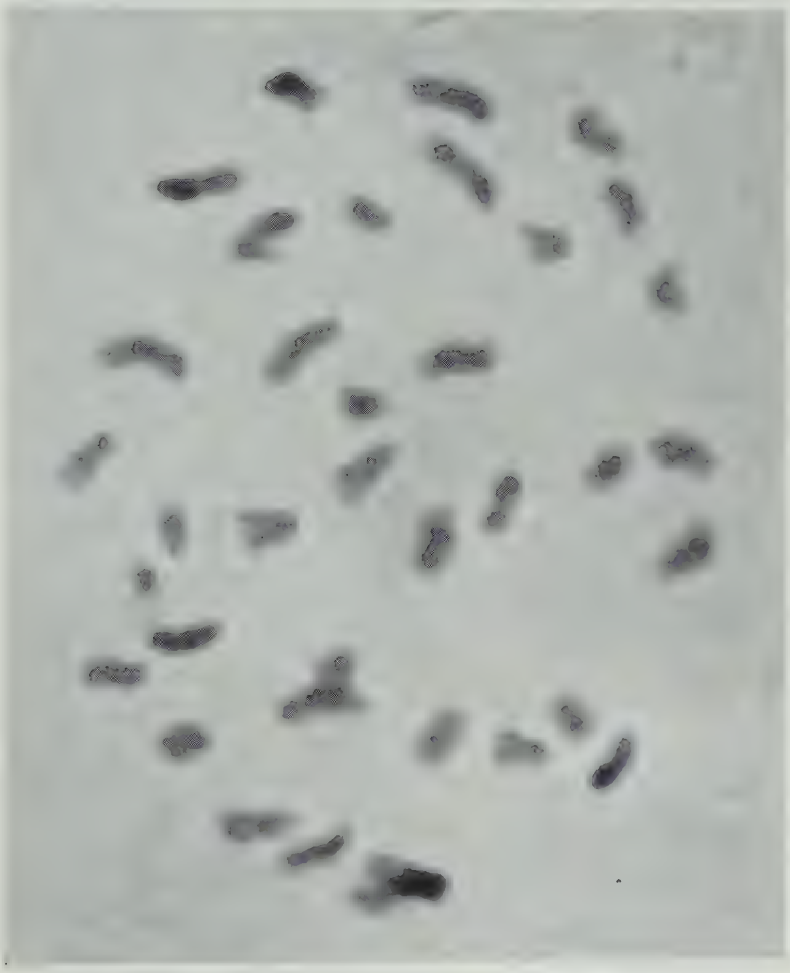
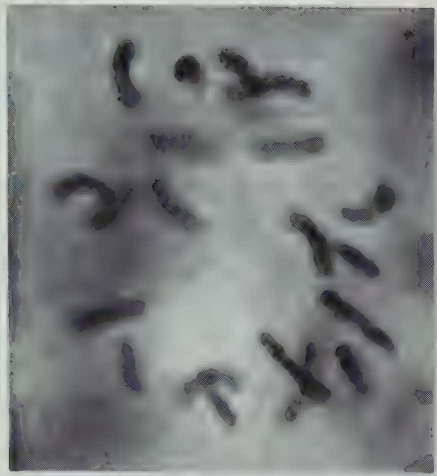


C. hamulata. Mitotic metaphase with $2n = 38$. Perm. Feulgen squash.

PLATE 2

a. C. platycarpa. Mitotic metaphase with $2n = 20$.
b. C. stagnalis. Mitotic metaphase with heterochromatic chromosomes. No cold pre-treatment.
c. C. platycarpa. Part of a metaphaseplate with 1 long and 1 small SAT-chromosome. For explanatory diagram see fig. 2.
d. C. platycarpa. Part of a metaphaseplate, with 1 long SAT-chromosome.
e. C. hamulata. Chromosome with median centromere.
f. C. palustris. First meiotic metaphase.
g. C. palustris. Second meiotic metaphase.
a-e. Perm. Feulgen squash.
f-g. From sections stained with crystal violet.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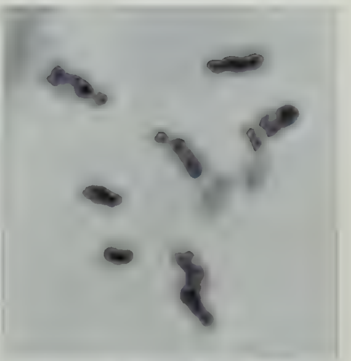
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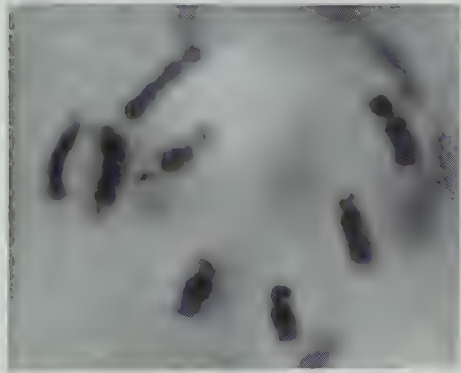
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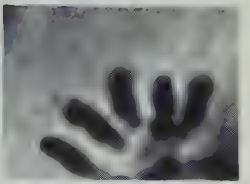
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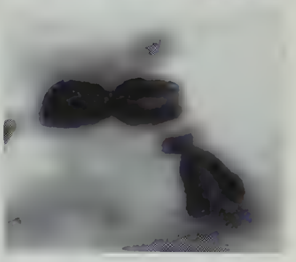
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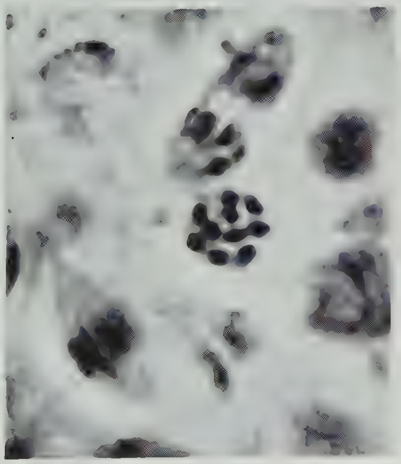
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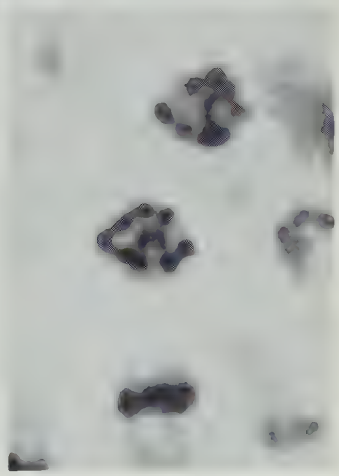
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PLATE 3

a. C. stagnalis. Mitotic metaphase with $2n = 10$. 0 SAT-chromosomes.
b. C. stagnalis. The same with 1 SAT-chromosome.
c. C. stagnalis. The same with 2 SAT-chromosomes.
d. C. obtusangula from the Isle of Texel (Netherlands). Mitotic metaphase with $2n = 10$. 0 SAT-chromosomes.
e. C. obtusangula from the prov. of Zeeland (Netherlands). Part of mitotic metaphase with 2 SAT-chromosomes.
f. C. palustris. Mitotic metaphase with $2n = 20$. 0 SAT-chromosomes.
g. C. palustris. The same with 2 SAT-chromosomes.
a-g. Perm. Feulgen squash.

PLATE 3

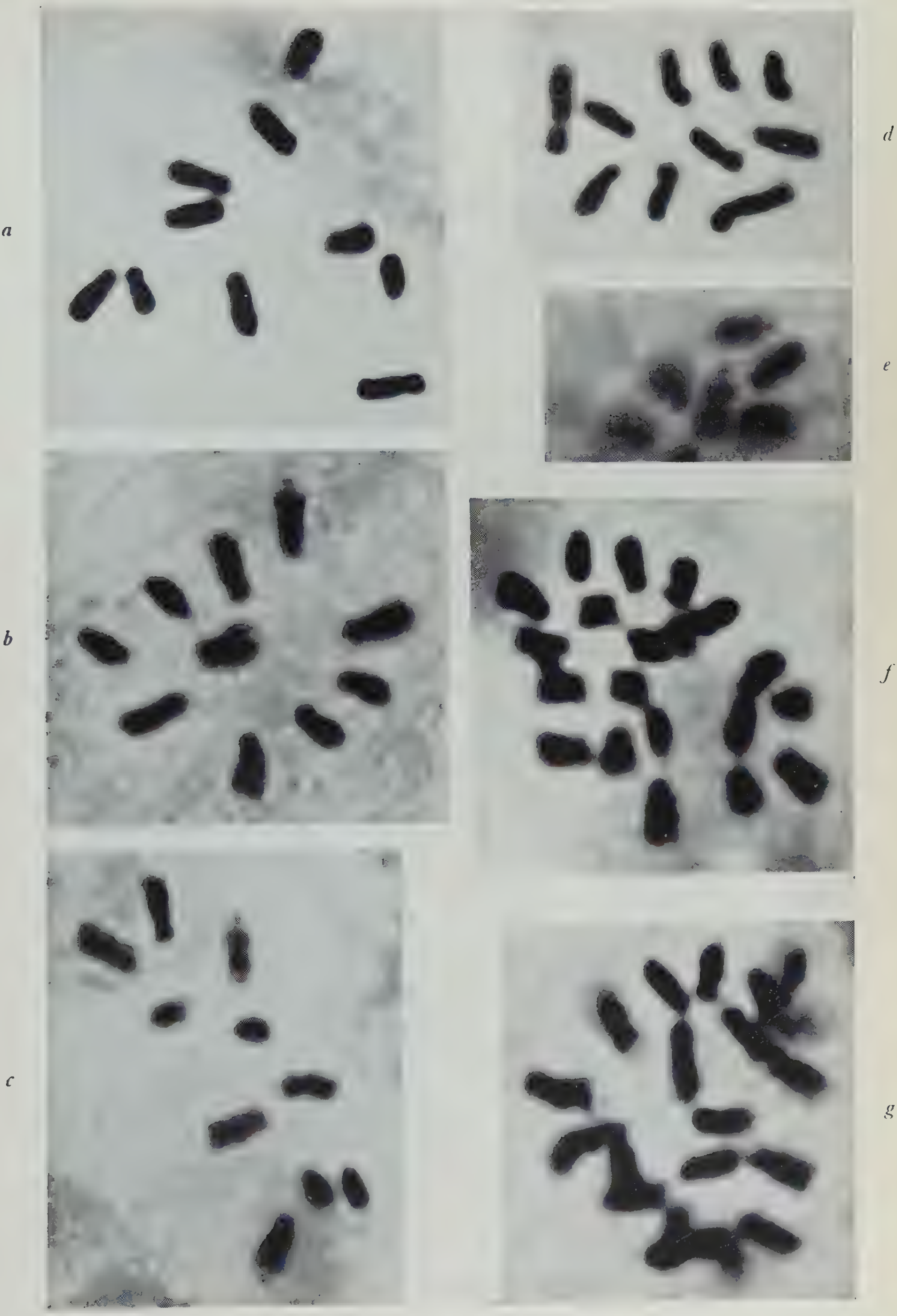


PLATE 4

a. C. stagnalis. Early mitotic prophase. The satellite consists of two parts. The connection with the end of the long arm of the chromosome is clearly visible.
b. Explanatory diagram of *a*.
c. C. stagnalis. The same as *a*. A small knob between the two parts of the satellites is visible.
d. Explanatory diagram of *c*.
e. C. obtusangula from the province of Zeeland (Netherlands). Late mitotic prophase. The two parts of the satellite just before joining.
f. Explanatory diagram of *e*.
a, *c*, *e*. Perm. Feulgen squash.

PLATE 4

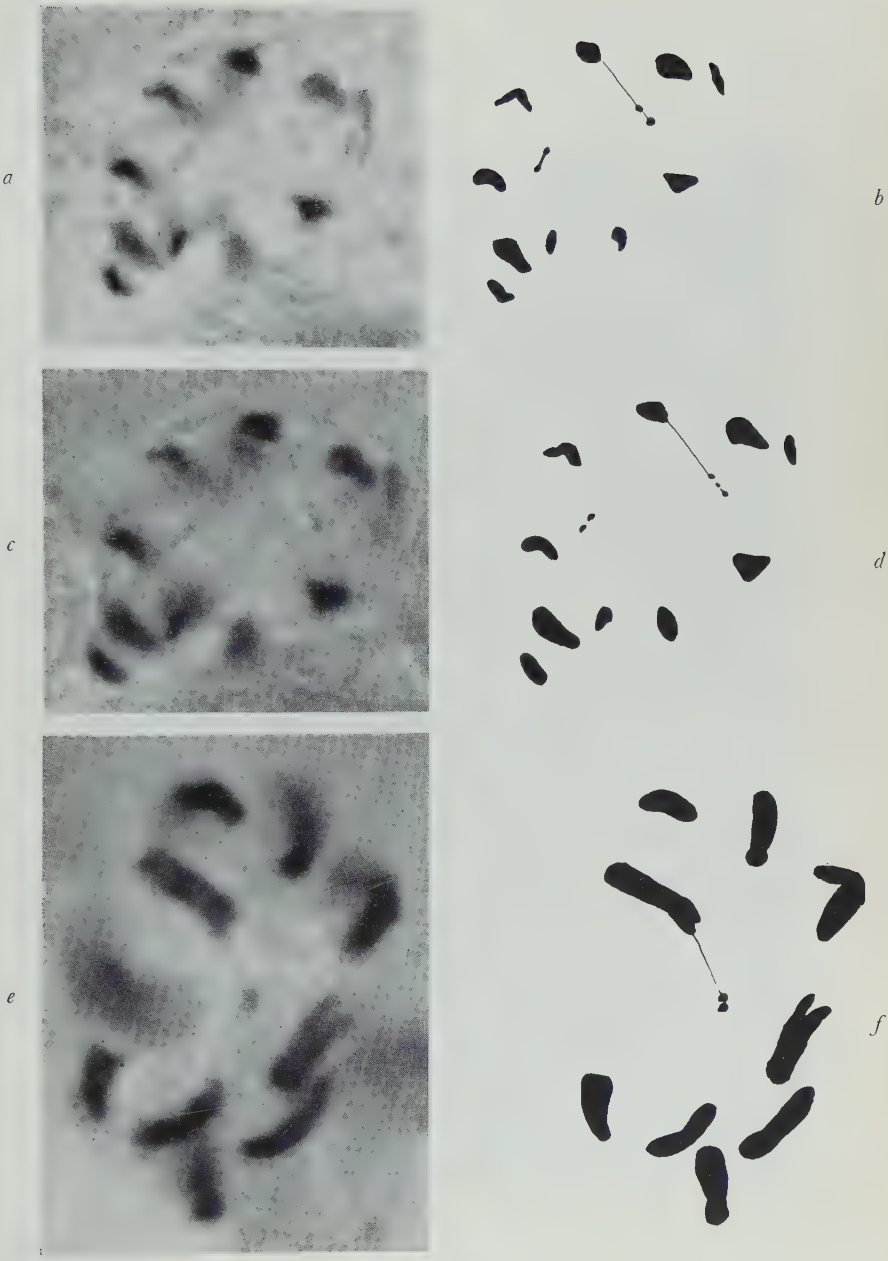
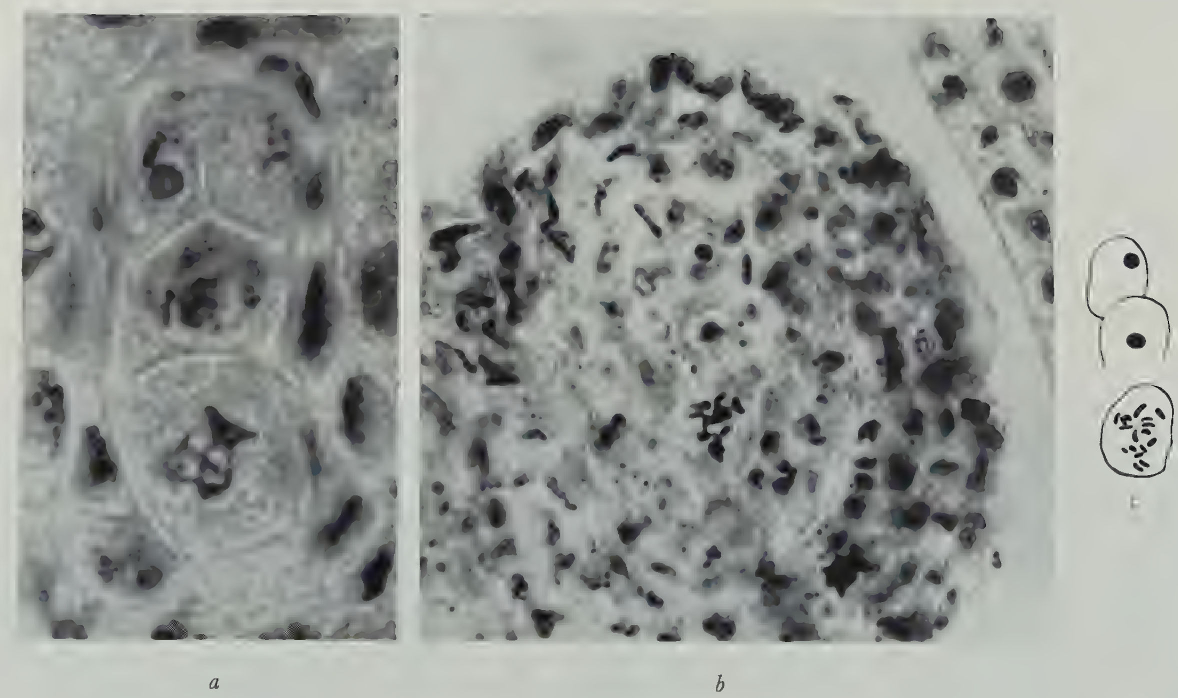
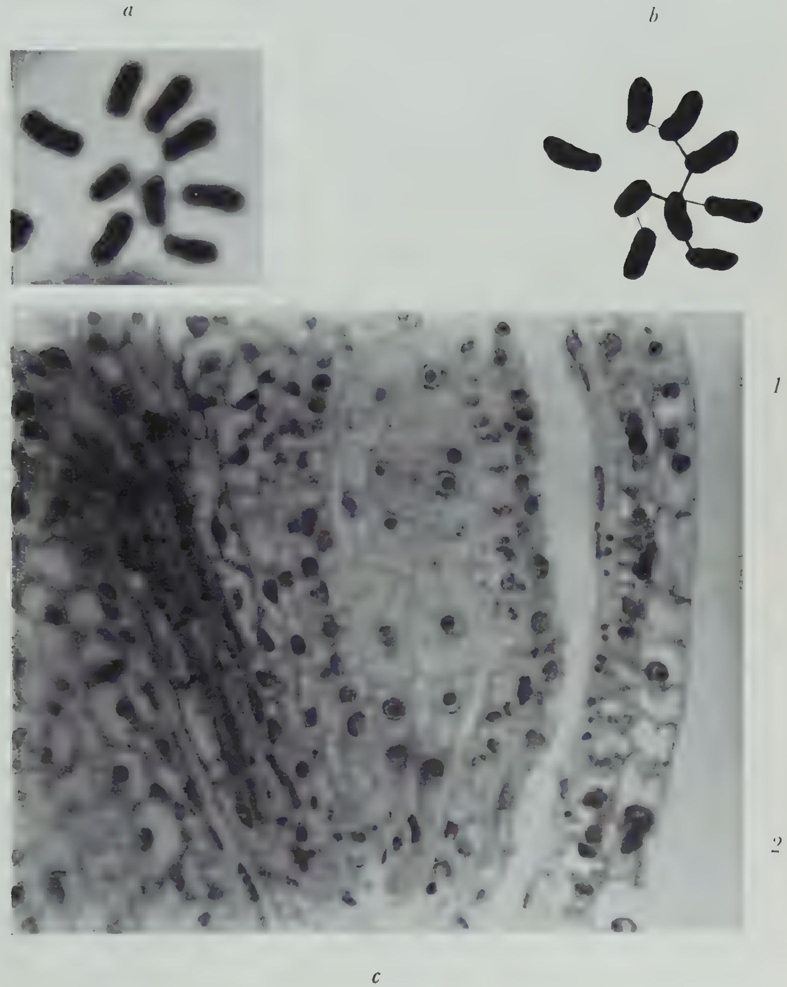


PLATE 5

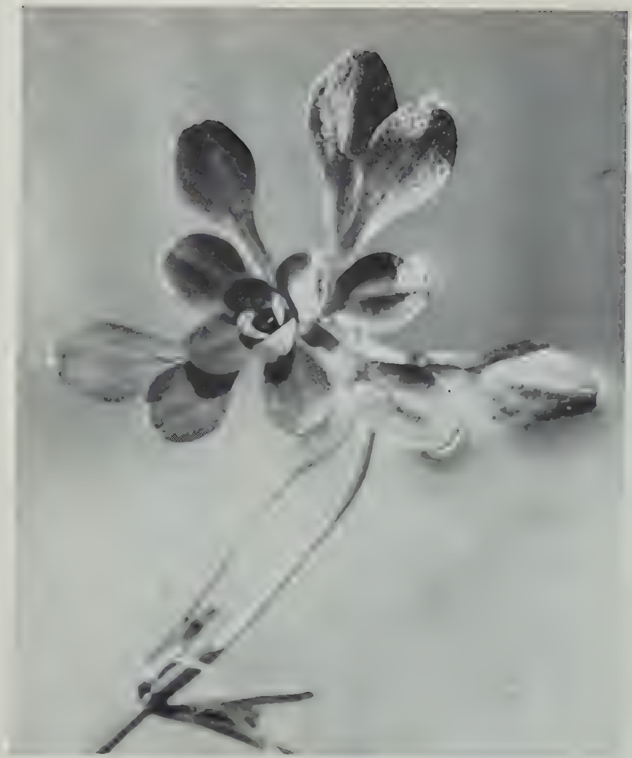


a. C. palustris. Longitudinal section of the ovule with T-shaped tetrad.
b. C. palustris. The same. Aposporous somatic cell near the base of the tetrad
c. Explanatory diagram of *b*. 17 chromosomes can be counted.
a and *b* stained with crystal violet.

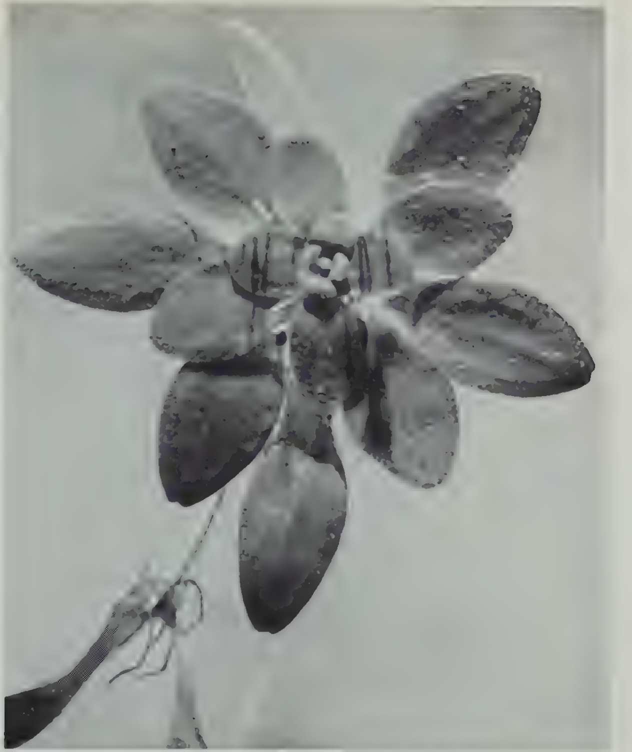
PLATE 6



a. C. palustris. Part of mitotic metaphase, showing the "threads" between the chromosomes. Perm. Feulgen squash.
b. Explanatory diagram of *a*.
c. C. palustris. Longitudinal section of the ovule, stained with crystal violet.
  1. young embryo surrounded by cellular endosperm.
  2. chalazal haustorium cells.



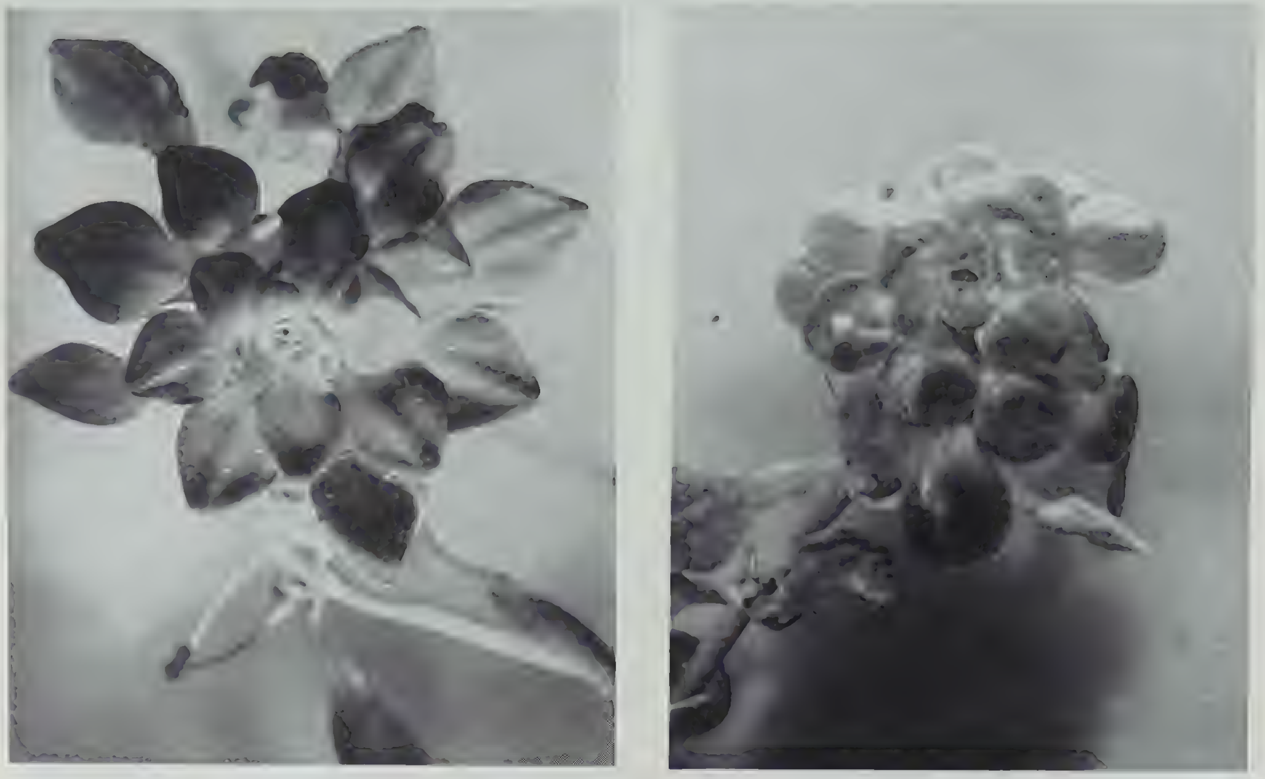
a



b

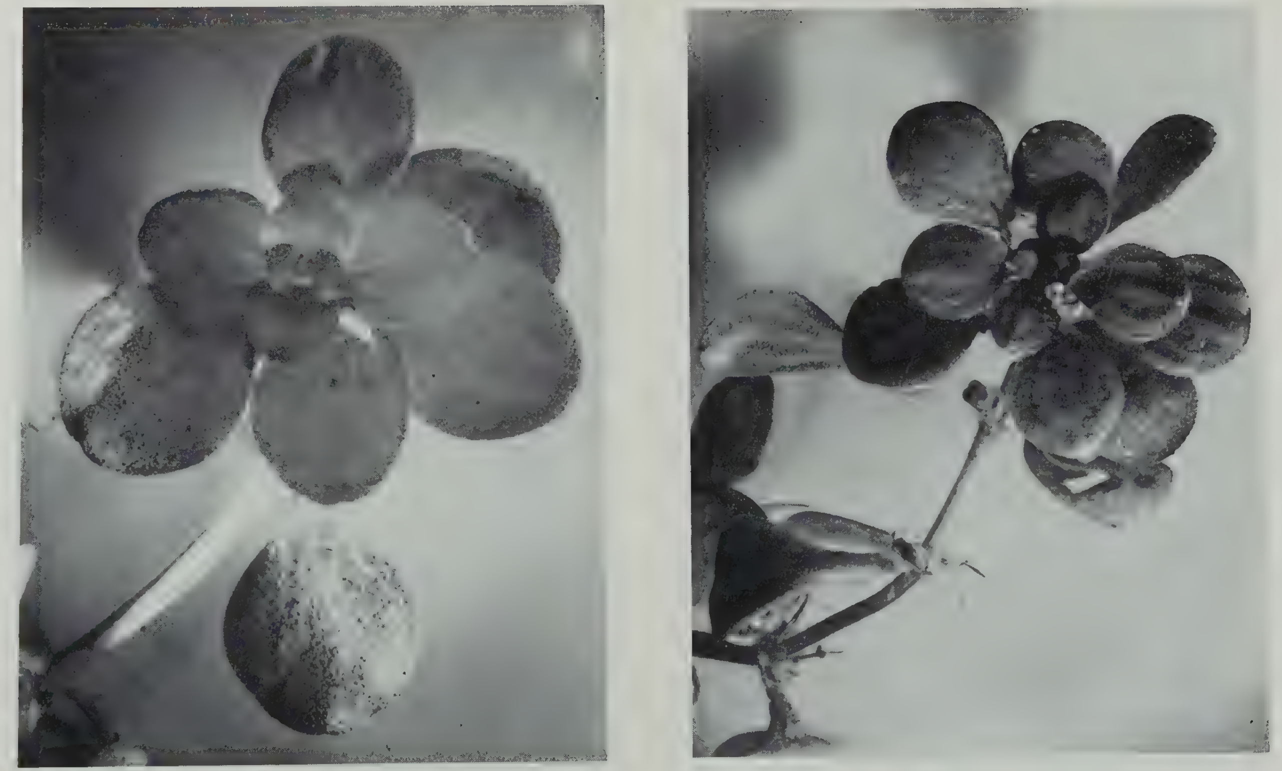
a. C. hamulata. Floating rosette of flowering plant. × 3½. *b.* C. platycarpa. Floating rosette of flowering plant. × 3½.

PLATE 8



a *b*

a C. obtusangula from the Isle of Texel (Netherlands). Floating rosette of flowering plant. × 3½.
b C. obtusangula from the province of Zeeland (Netherlands). × 3½.

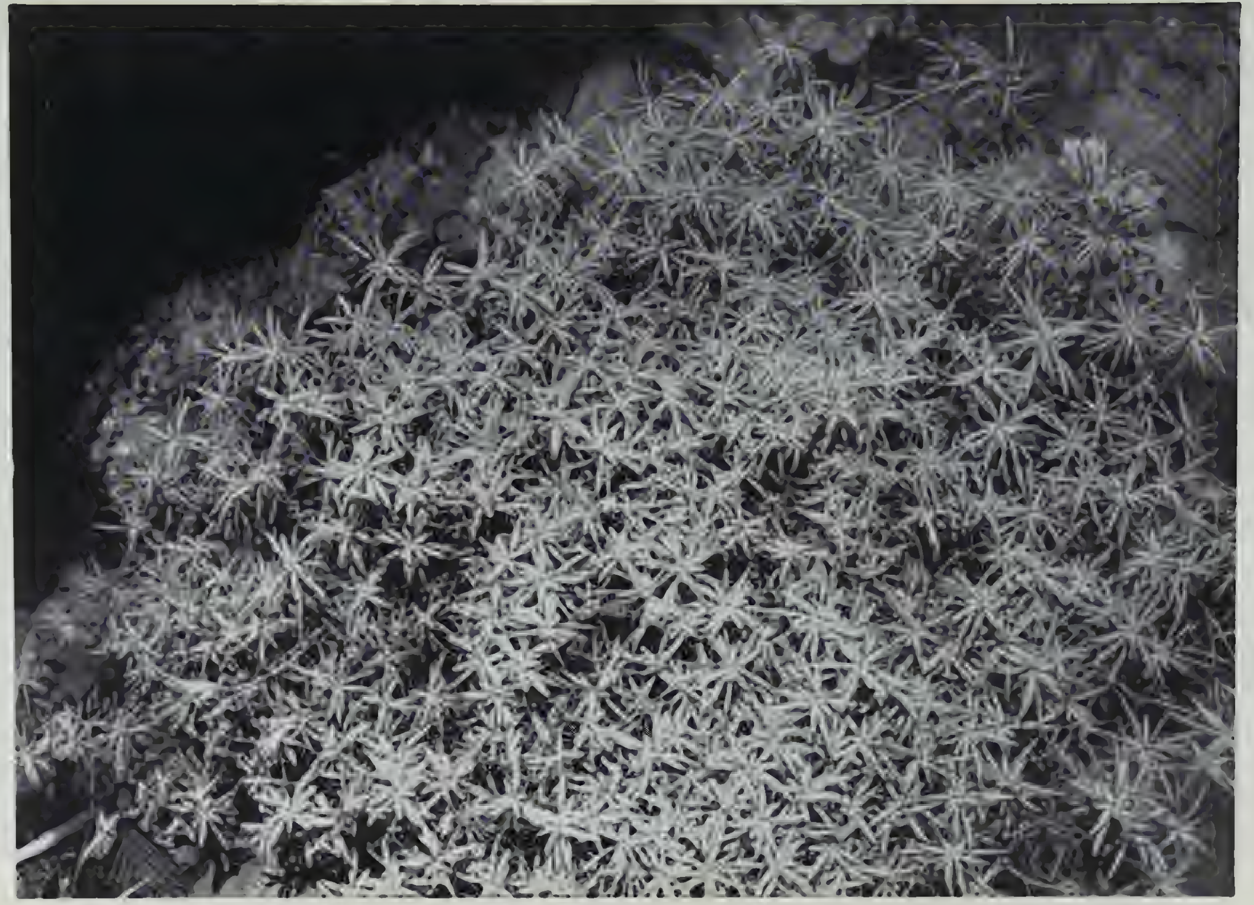


a

b

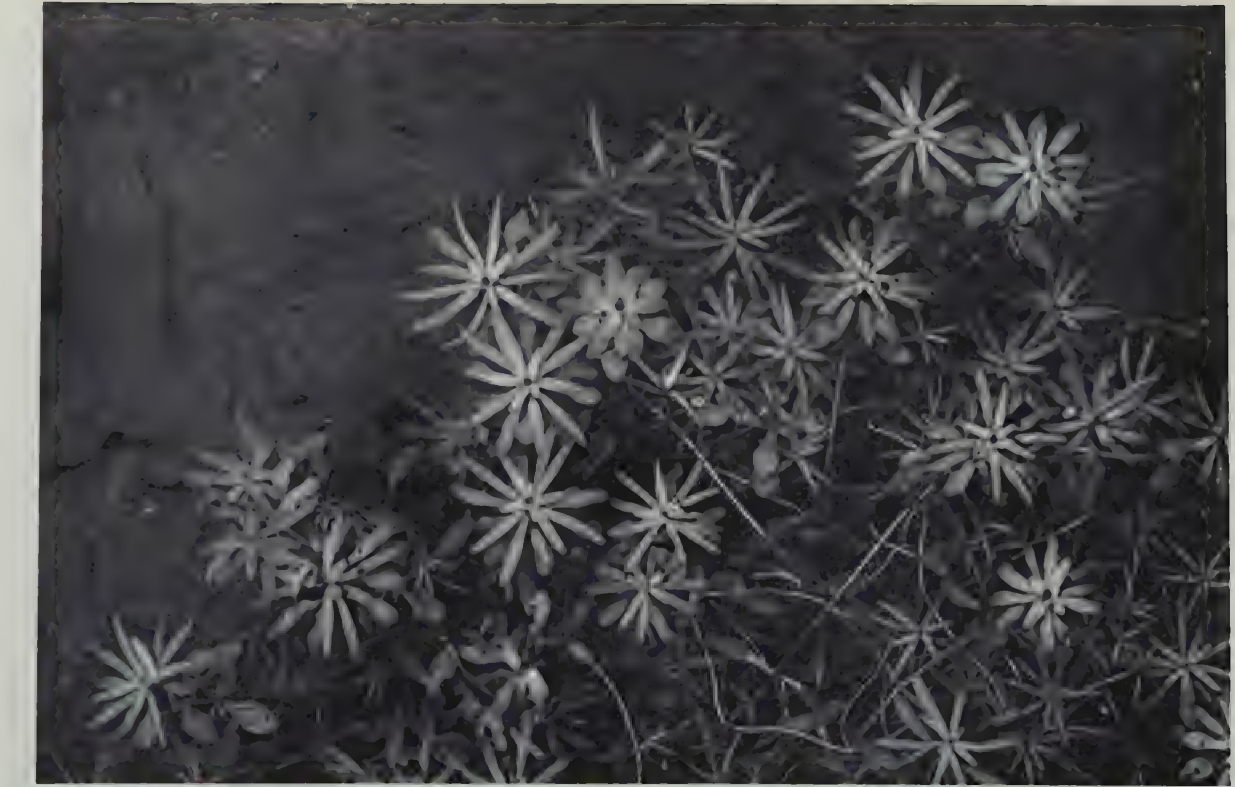
a. C. stagnalis. Floating rosette of flowering plant. × 3½. *b.* C. palustris. Floating rosette of flowering plant. × 3½.

PLATE 10



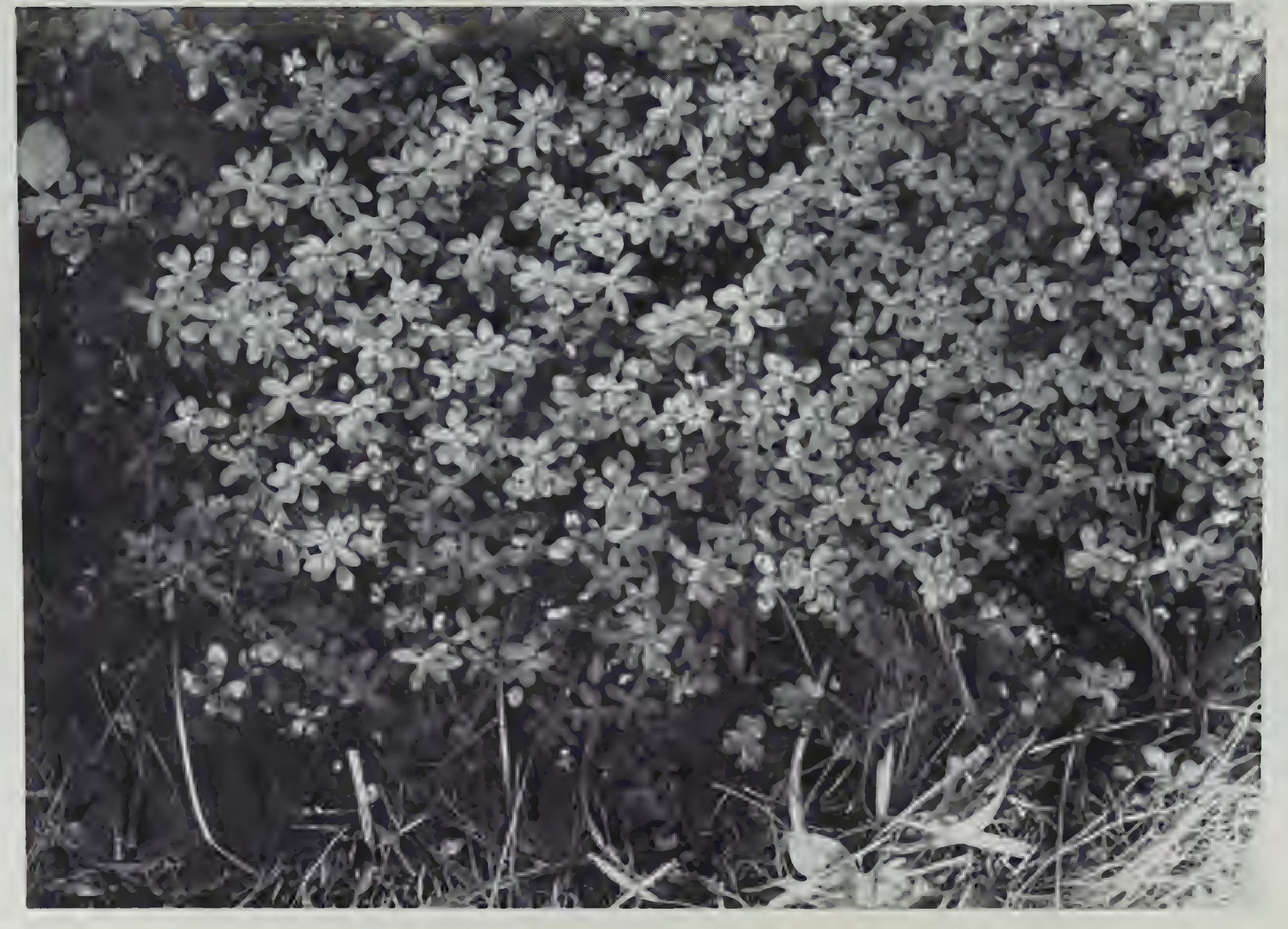
C. obtusangula. Waterform in winter. ½ × nat. size.

PLATE 11

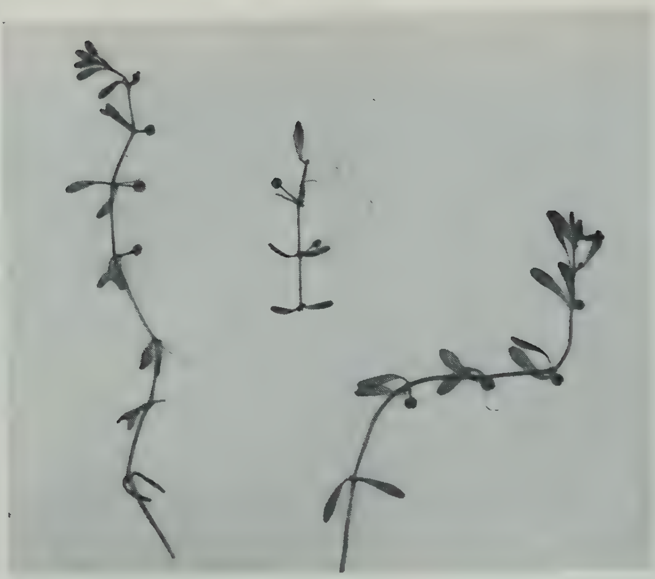


C. obtusangula. Waterform in autumn, $^1/_4$ × nat. size. In the middle: summerrosette with rhomboid leaves, other branches with linear winterleaves.

PLATE 12



C. platycarpa. Waterform in early summer. Floating rosettes with elliptical leaves. $^{2}/_{3}$ × nat. size.

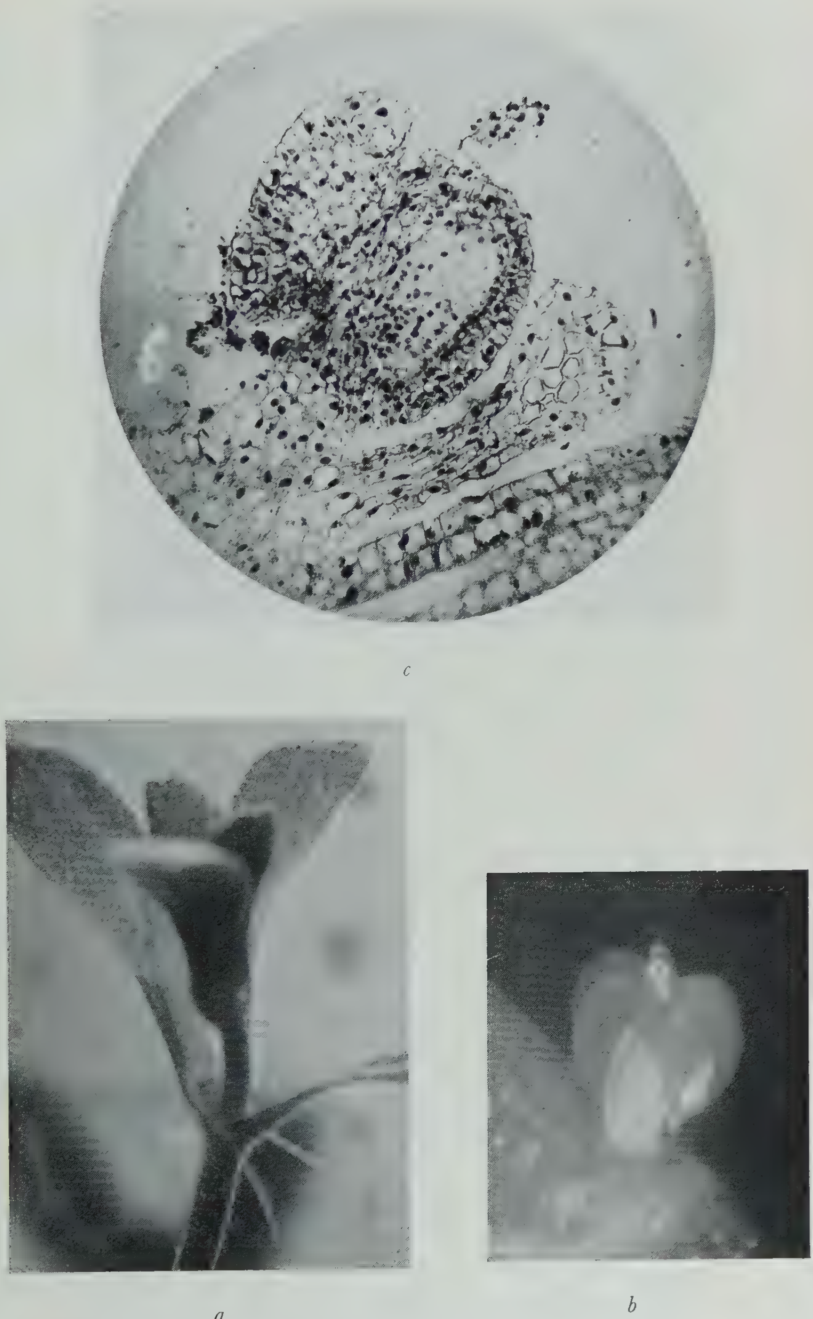


a

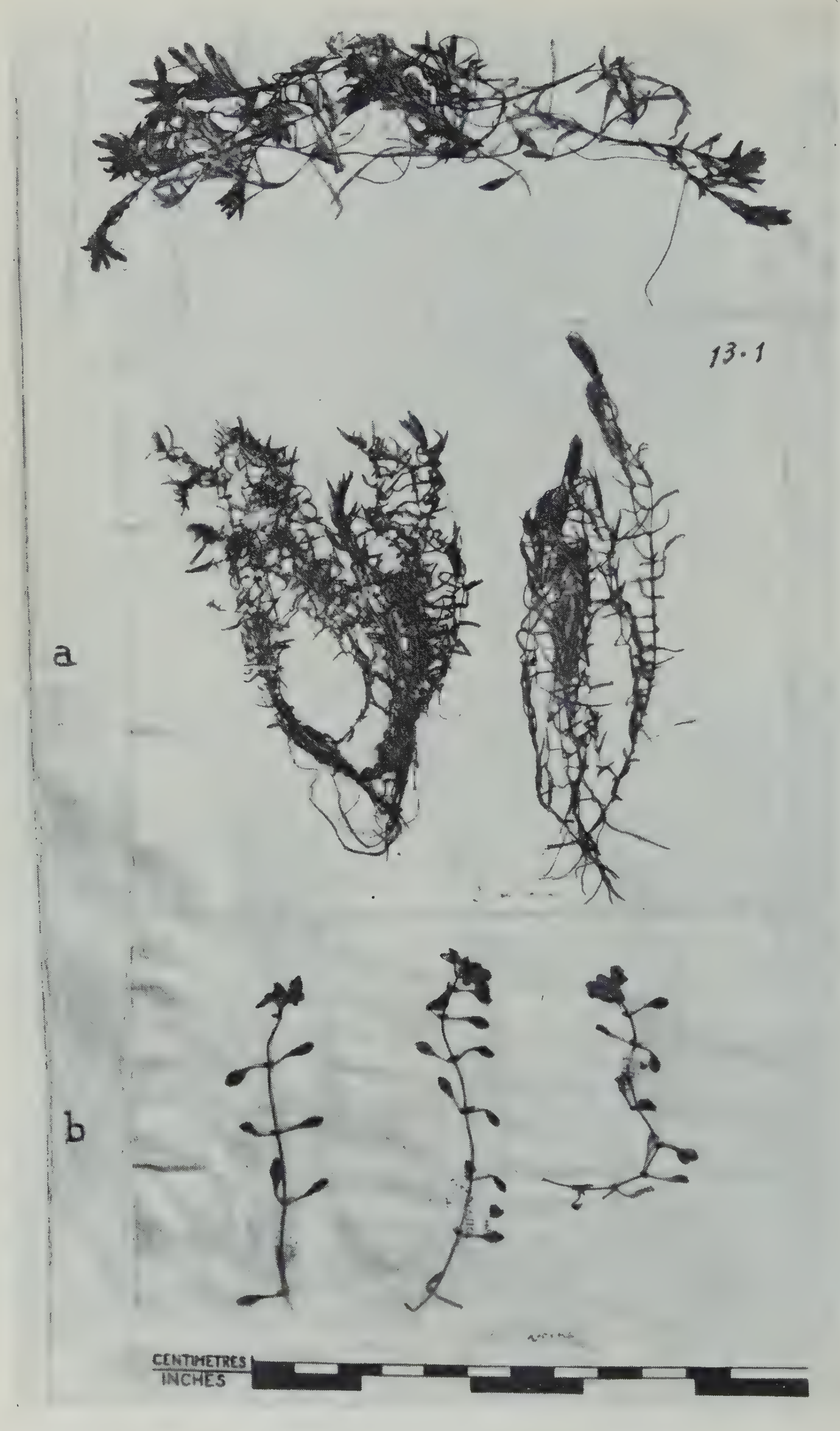
b

a. C. hamulata. Landform with stalked and sessile fruits. Nat. size.
b. C. platycarpa. Landform. Nat. size.

PLATE 14

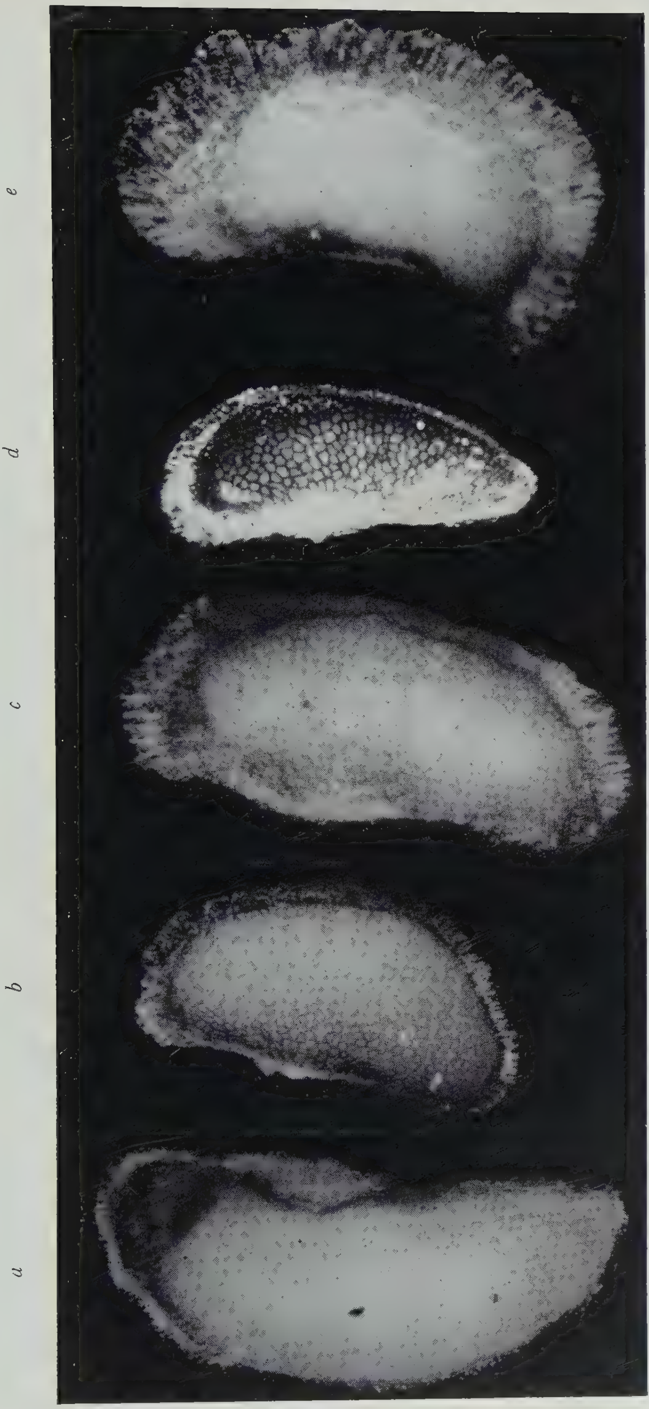


a. C. hamulata. Waterform. In the left leafaxil the female flower with reflexed stigmata, in the other leafaxil the young anther. × 7½.
b. C. palustris. Landform. Female flower with reduced stigmata. × 20.
c. C. palustris. Longitudinal section of a leafaxil with two flowers. × 45. On the left: pistil with partly reduced stigmata. On the right: reduced stamen with only a few pollengrains. Stained with crystal violet.



Herbarium specimens of Linné (Linnean Society, London). *a.* C. hermaphroditica Juslen. (C. autumnalis L.). *b.* C. palustris L. (C. verna L.). For explanation see p. 359.

PLATE 16



Seeds. × 50. *a*. C. obtusangula, *b*. C. hamulata, *c*. C. platycarpa, *d*. C. palustris, *e*. C. stagnalis.

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FIBRILLAR ARCHITECTURE OF GROWING PLANT CELL WALLS

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With Plates 17—23

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INTRODUCTION

In an earlier communication (13) the present authors published electron micrographs of the cellulose texture in the primary cell wall of growing hairs of *Gossypium*, *Ceiba* and *Asclepias*. The micrographs showed that, in general features, the structure of these hairs resembled the structure previously found in the growing cell walls of *Tradescantia* staminal hairs (12) and *Phycomyces* sporangiophores (11). Common to all was a compact transverse fibrillar structure on the inner side. The outer side, with cotton hairs, had an axial orientation of the fibrils and in between the two a more or less random orientation seemed to occur. With *Phycomyces* and *Tradescantia*, however, the outer fibril layer was isotropic.

As an explanation of this architecture a theory, named *multi-net-growth theory*, was proposed (13). It necessitated three assumptions,*viz.*:

1. The cell walls studied were growing until the moment of fixation and hence, all cell wall layers were extending axially until fixation.
2. New fibrils are deposited onto the inner face of the cell wall. This involves that every layer of fibrils of the same age is gradually shifting outwards.
3. On being extended axially each of the transversely oriented layers on the inner side of the cell wall behaves like a network consisting of intertwined fibrils.

Extension of the cell wall, as assumed in 1 and 3 involves reversion of fibril orientation, *viz.*, in the outer layers, from isotropic to more nearly axial, and in the inner layers, from transverse to more nearly isotropic and eventually also to more nearly axial. In this respect every layer of fibrils behaves like a net.

The twines of this net, however, should not be imagined to be tied together with fixed knots but merely to overcross, hence able to slip past one another. FREY-WYSSLING has pointed out that reversion of fibril orientation from transverse to axial involves a reduction of cell diameter, except if the fibrils slip past one another. Since the growing cells examined either widen or retain their original width, reversion of fibril orientation involves slipping of the fibrils.

In this paper we studied growing tips and evidence will be presented of the orientation of the outermost fibrils being actually changed in the course of cell wall extension. The diameter of the cells examined does not decrease, so the fibrils do slip past one another.

The three assumptions also involve that the transverse orientation on the inner face of the cell wall must gradually merge via an isotropic into a more nearly axial orientation on the outer face.

According to 2. the fibrils of the outermost layer, like those of the other layers, have been deposited onto the inner face of the cell wall at an earlier stage. So this layer is the oldest one in any part of the cell wall at any moment. In cells with a growing tip, as presumably the cotton hair, this layer must have originated on the inner side of the tip; in cells lacking a growing tip, *e.g.*, *Phycomyces* sporangiophores, however, it must have originated at the apical end of the growth zone.

As regards assumption 1.: with *Phycomyces* sporangiophores and with young *Tradescantia* cells we were certain that the electron micrographs actually represented growing cell walls, but the other hairs might grow at their apex only, whereas the micrographs represented a portion of the tubular part. Only from the negative double refraction, wich implies that a secondary cell wall had not yet developed, it was deduced that the tubular part had not stopped elongating. Although, as far as we know, there are no exceptions to the rule, it offers no proof [1]). At present, however, we can point to the results of O'KELLEY (8), which make very probable that the cotton hair grows over its entire length. He wrote us (9): "If cotton fiber size is plotted against time .... the (growth) curve is a typical S-curve. This . . . . indicates that more of the fiber is concerned with elongation as the fiber gets larger, until growth is slowed down for other reasons. This is not compatible with tip growth".

METHODS

In this work we used the same methods of cleaning, mounting and shadowing of the cell walls as have been described in our previous paper (13).

RESULTS

A. COTTON HAIRS

The hairs examined belonged to the sample used before (13). A hair tip, enlarged 30.000 x, is shown in plate I. A full grown cotton hair of 2,5 cm would have a lenght of 750m when enlarged to this scale. The network of cellulose fibrils completely envelops the tip; apparently it is nowhere perforated. Plates 18a and b show 40.000 x enlargements of two areas of Plate 17. On the semispherical tip the fibrils are oriented at random, but as soon as the tip merges into the tubular part axial orientation prevails, becoming more evident along the next 10 μ down.

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[1]) Wide tubular cells like vessels stay negatively birefringent since the secondary cell wall is transversely oriented. *Tradescantia* hairs, also with rather wide cells, likewise retain their negative double refraction. The correlation only holds for cells with an axially oriented secondary wall; the other hairs examined belong to this category.

The same features are shown in plate 19.

To our mind, the apparent thickness of the cell wall and the fact that it is surrounded by air are incompatible with new fibrils being deposited on its outer face. This implies that the axially oriented fibrils of the tubular part were situated at the tip of the hair at an earlier stage and then were oriented at random.

Why should the change of fibril orientation from isotropic into axial coincide with the merging of the semi-spherical tip into the cylindrical part of the hair? Obviously, because in the tip, cell wall extension is not confined to the axial direction. This is visualized by a schematic drawing (fig.1). Sectors have been drawn in what represents the tip, and in the right part of the figure the extension of an area originally situated near the extreme tip, is illustrated. Axial extension prevails, but the width of the area also increases.

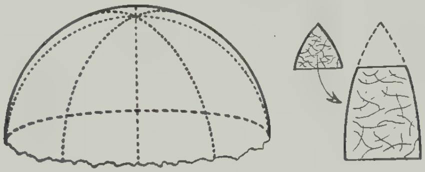


Fig. 1. Schematic illustration of multilateral cell wall extension in the tip of a growing cotton hair.

According to polarisation microscopical observations the semi-circular part of the flattened tip is not isotropic as is the randomly oriented fibril texture on the outer face, but it is negatively birefringent with reference to the cell axis. Therefore, transversely oriented fibrils like those found on the inner side of the wall in the tubular part (13) must occur in the tip as well. Probably only the central area of the extreme tip is isotropic both on the outer and on the inner side. (fig. 4). The newly deposited fibrils will rapidly shift outwards, since the extension of the cell wall requires a continuous generation of new fibrils all of which will be deposited onto the inner face of the cell wall. Meanwhile the older layers will acquire random orientation.

This concept is illustrated in fig. 2A. Here, as well as in B and C, distinct layer boundaries are drawn, but this has been done for illustrative purposes only. In reality, however, every layer merges into its neighbours (13, fig. 7 and 8). In fig. 2B the mean orientation of the fibrils of the outermost layer is supposed to have become axial. Evidently, the elongation of the part of the cell wall they belong to, causes the layer to grow thinner. According to our hypothesis the inner layer in

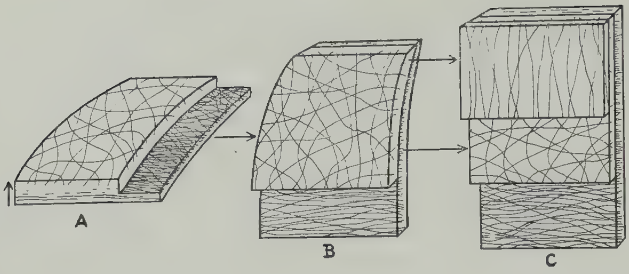


Fig. 2. The fibrillar structure in the growing cotton hair. A: near the top, B: where the tip merges into the tubular part, C: in the tubular part. Layer boundaries are drawn for illustrative purposes only; the transition is gradual.

B will gradually shift to the periphery and will acquire a random, or perhaps even a more nearly axial, orientation.

B. ROOT HAIRS OF *Zea mays*

Corn seeds were germinated in moist air. The root hairs were cut off and prepared as usual.

Plate 20a shows the outer faces of the tip of a root hair; plate 20b shows both the inner and outer faces of the cell wall at the cut end somewhere below the tip.

The outside layer of the root hair, unlike that of cotton hairs, retains an isotropic structure when getting older and more distant from the tip. Onto the inner face of this layer a layer of axially oriented fibrils is deposited. On looking at the inner face of the cell wall on plate 20b one will observe that the fissures in the latter layer reveal the lack of transverse fibrils as would have been comparable with those found in cotton hairs.

Most root hairs are known to grow at their tips only. The axially oriented inner layer obviously is the secondary cell wall. Polarisation microscopy shows that it is deposited from just below the tip downwards. This is in line with growth being limited to the tip. The isotropic structure of the tip is retained downwards because the tubular part does not grow. The latter fact is also in line with transversely oriented fibrils lacking.

On plate 20a some loose fibrils and several thick fibril bundles may be noticed at the tip. However, we did not find the 1 μ thick felt-like layer of fibrils, wich was reported by FREY-WYSSLING and MÜHLETHALER (3) to cover the cell wall proper at the tip. The method of cleaning of the hairs as used by these authors (10 % HCl, boiling 15 % NaOH) may have been too drastic. In other respects their results are corroborated by us.

C. STELLATE CELLS OF *Juncus effusus*

Multi-net-growth being established in free growing epidermal hairs of cotton and the like, a similar architecture of the cell wall was looked for in parenchymatous cells. If in any, it might be found in the wall of cells bounding on intercellular space, for here conditions are comparable to those cotton hairs are subject to. In both cases the cell walls should be thick enough to withstand turgor pressure in contrast with cell walls between adjacent meristematic cells.

The stellate pith cells in the meristematic bases of the leaves (so-called stems) of *Juncus effussus* were chosen because the arms of these cells are in similar conditions as young cotton hairs. Both of them grow free in an air-filled space, the difference being that the tip of each cell arm of the *Juncus* cell meets the tip of the corresponding arm of an adjacent cell.

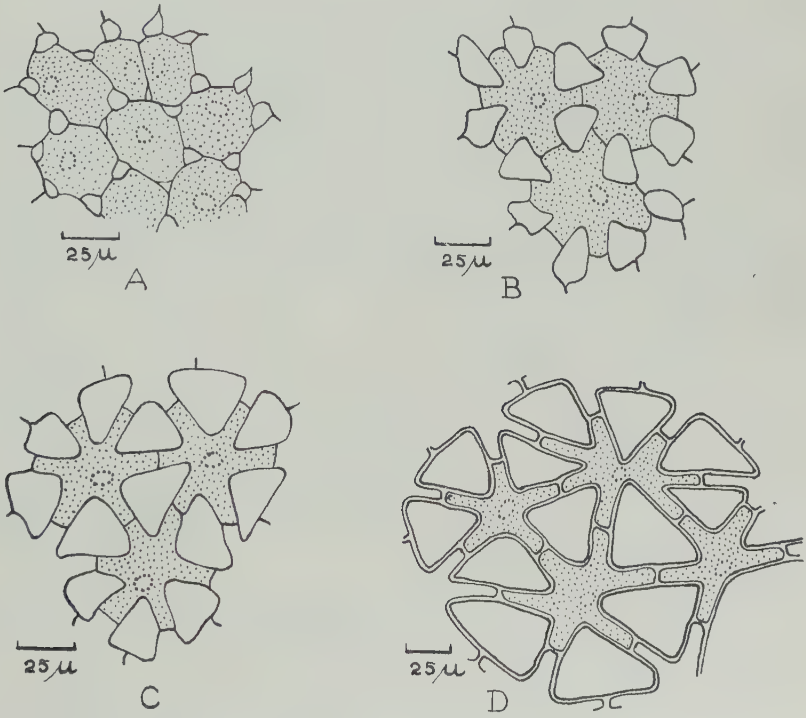


Fig. 3. Redrawn from Maas Geesteranus (6). A, B and C: growing stellate pith cells of *Juncus* leaves. D: full grown cells.

Maas Geesteranus (6) described the genesis of the stellate cells and the big intercellular space between them. Fig. 3 has been redrawn from this writer's paper. Cells like those examined in the present work are represented by fig. 3B and C. The arms of the cells are lengthening and, accordingly, prove to be negatively birefringent, as also are growing tubular cells like hairs. Arms of full grown cells, however, are positively birefringent because of the secondary wall which is oriented parallel to the arm axis.

Cells at stages B and C are found only in a zone of *ca.* 1 cm length at the base of growing leaves. The basal end of this zone was located by examining between crossed nicols cross-sections of the leaf, starting with a section through the meristematic zone, and proceeding in apical direction until a section with cells at stage B had been obtained. Then, the upper end of the zone was found by examining a cross section *ca* 1,5 cm from the basal end and proceeding downwards until cells at stage C had been found. Thereupon the pith was removed, frozen, and cut into 15 μ sections with a freeze microtome. The sections were cleaned as usual. By this process many cells got free.

In plate 21 one arm and a portion of the central part of the cell are shown; the arm of the adjacent cell has broken off from the latter at its base. Plate 22a represents the joint of two corresponding arms. The cells must be at stage B, for the arms are rather short.

Plate 22b represents a similar joint of cells at stage C.

Clearly the fibrillar network of the (longer) arms of older cells is axially oriented as contrasted with the isotropic layer on the outer side of the (shorter) arms of younger cells. The altered orientation can only be ascribed to cell wall extension, unless it is supposed that fibril deposition is not confined to the inner side of the cell wall and that new fibrils have been deposited on the outer side. This supposition, however, seems to us untenable because of the cell wall being rather thick and bounding on the intercellular space. Moreover, judging from Häusermann's results (5) with similar cell walls, it should be slightly cutinized.

The joints of the rounded ends of the cell arms are enveloped by many fibrils linking up one arm with the other. The micrographs suggest that this fibrillar sheath is detached from the fibril layers of the cell wall proper. Probably these fibrils originate from the cell wall of the mother cell, but this explanation is not entirely satisfactory. Although several free fibril ends appear in the micrographs, nothing indicates that cellulose fibrils should have been dissolved (see Frey-Wyssling and Mühlethaler (4).

The negative double refraction of growing arms is caused by a transverse fibril layer on the inner side of the cell wall, as is shown on plate 23a Randomly oriented fibrils show up between the axial outer, and the transverse inner layers.

Plate 23b shows peculiar fibril bundles which have often been found on the outer side of the central part of the pith cells. These bundles cannot be supposed to have originated by disconnection of arm joints. Though lying flat on the cell wall in the desiccated preparation they are completely free from the wall except at their bases. They may be artefacts formed by aggregation of loosened fibrils. If not, these funnel-shaped structures may have been formed by plasmodesms. We have not found an explanation satisfying both of us.

Both the outer side and the inner side of the cell wall of the central part of the cell are isotropic. This is in line with its multilateral growth.

DISCUSSION

The multi-net-growth hypothesis, aiming as it does at explaining by unilateral growth, the different cellulose fibril textures on the inner as compared with the outer side of the walls of many plant cells, should be based on observations on extending cell walls. In our previous work on the cell walls of cotton and other hairs (13) we missed the tips of the hairs and so we had to *assume* that the texture we studied was a product of cell wall extension, but now, with young *i.e.* growing cotton hairs, the tips as well have been examined.

Cotton hair. The outermost fibril layer is isotropic at the tip proper, but it is axially oriented further down along the cylindrical part of the hair, with a gradual transition from isotropic to axial orientation. Since deposition of fibrils onto the outer face of the cell wall is unlikely, a gradual re-orientation of these fibrils, while drifting away from the tip, seems well established. It has been argued already (p. 386) that reversion of fibril orientation should involve a change in cell diameter unless the fibrils are free to slip past one another. So they must be, for reversion of fibril orientation was proved to happen in a cell of constant diameter. Thus the cellulose texture in the cell wall is not as firm and inextensible as it appeared to FREY-WYSSLING and collaborators when they rejected the idea of cell wall extension as a major factor in growth, retaining it merely for exceptional cases, *e.g.*, the onset of a local outgrowth of a cell or the widening of vessels (1). Trylu the primary cell wall looks a very entangled network, but it should be recalled to mind that FREY-WYSSLING (2) again, pointed out that the structure is very loose, the cellulose fibrils representing only 2,5 % by weight of the primary cell wall. Undoubtedly hemicellulose, pectin and water fill up the space between the fibrils. Recently RÅNBY (10) found that the adhesion of the cellulose fibrils is very much reduced by hemicellulose. These considerations may help to imagine fibrils slipping past one another.

In order to visualize the behavior of the fibrils in the cellulose network we may compare the latter with a tangle of fresh, filiform algae spread on a glass plate. The algal threads, though frequently intertwined, will freely slip past one another. The tangle can be extended at will and the threads will become oriented accordingly.

As a consequence of the second one of the three assumptions mentioned in the Introduction, *viz.*, that new fibrils are deposited onto the inner layer of the cell wall, the origin of the outermost fibril layer should be discussed. Confining ourselves for the present to cotton hairs, we may state that these fibrils must have been deposited in the central area at the extreme apex of the semispherical tip of the hair. Here growth is multilateral, and fibrils in the inner layer of the cell wall probably are oriented at random as are those in the outer layer. On shifting outwards any area will stay isotropic until, getting farther and farther away from the centre, and in regions where growth is mainly axial, the fibril layer becomes more and more axially oriented.

Returning to the inner side of the cell wall at the tip, we may expect that here as well, *growth* in any area is the more axially directed the farther from the tip the area is situated. Now, the cytoplasm is known to react to unilateral — here axial — growth, by depositing the fibrils transversely with respect to the direction of growth. The negative double refraction at the tip shows that this also applies with cotton. If the inner face of the cell wall at the tip of the hair could be examined, a gradual, but maybe rather fast transition from isotropic to transverse apposition of fibrils would be found. Fig. 4 may serve to illustrate our views on the fibril orientation at the extreme tip.

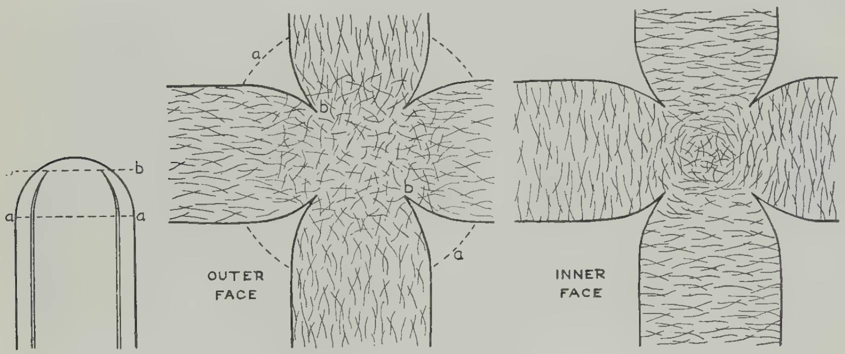


Fig. 4. Fibrillar architecture of the outer and inner faces of the tip of the cotton hair.

Assumption 3 reads: "On being extended axially each of the transversely oriented layers on the inner side of the cell wall behaves like a network consisting of intertwined fibrils".

Whereas any fibril layer, if isotropic, on being extended unilaterally, must show a change of the orientation of the fibrils, this needs not occur in case the fibrils run parallel to one another and transversely with respect to the direction of growth. The micrographs of the inner side of cotton hairs (13) and of *Juncus* cell arms (plate 23a), however, show that the fibrils are not exactly parallel. Instead, the inner layer looks like a net with transverse meshes. Every fibril will be intertwined, though very loosely, with several fellow fibrils of the same generation.

No reason can be devised why slipping of the fibrils past one another should not happen in the inner layer of the cell wall like it has been shown to occur in the outermost layer. Incrustation with cutine and lipoids is less likely to have occurred in the inner part of the cell wall than in the outer part. So, no objection on account of the fibrils having to slip, can be raised against our assumption 3.

Hence the fibrillar texture of the cell wall of the cotton hair can be completely explained by the multi-net-growth hypothesis.

Juncus stellate cell arms have no growing tips. Growth along an annular zone should be responsible for cell arms coming into being. From the very first, growth is unilateral. The growth zone lengthens considerably; in fact the whole of the cell all of the arm is nothing but

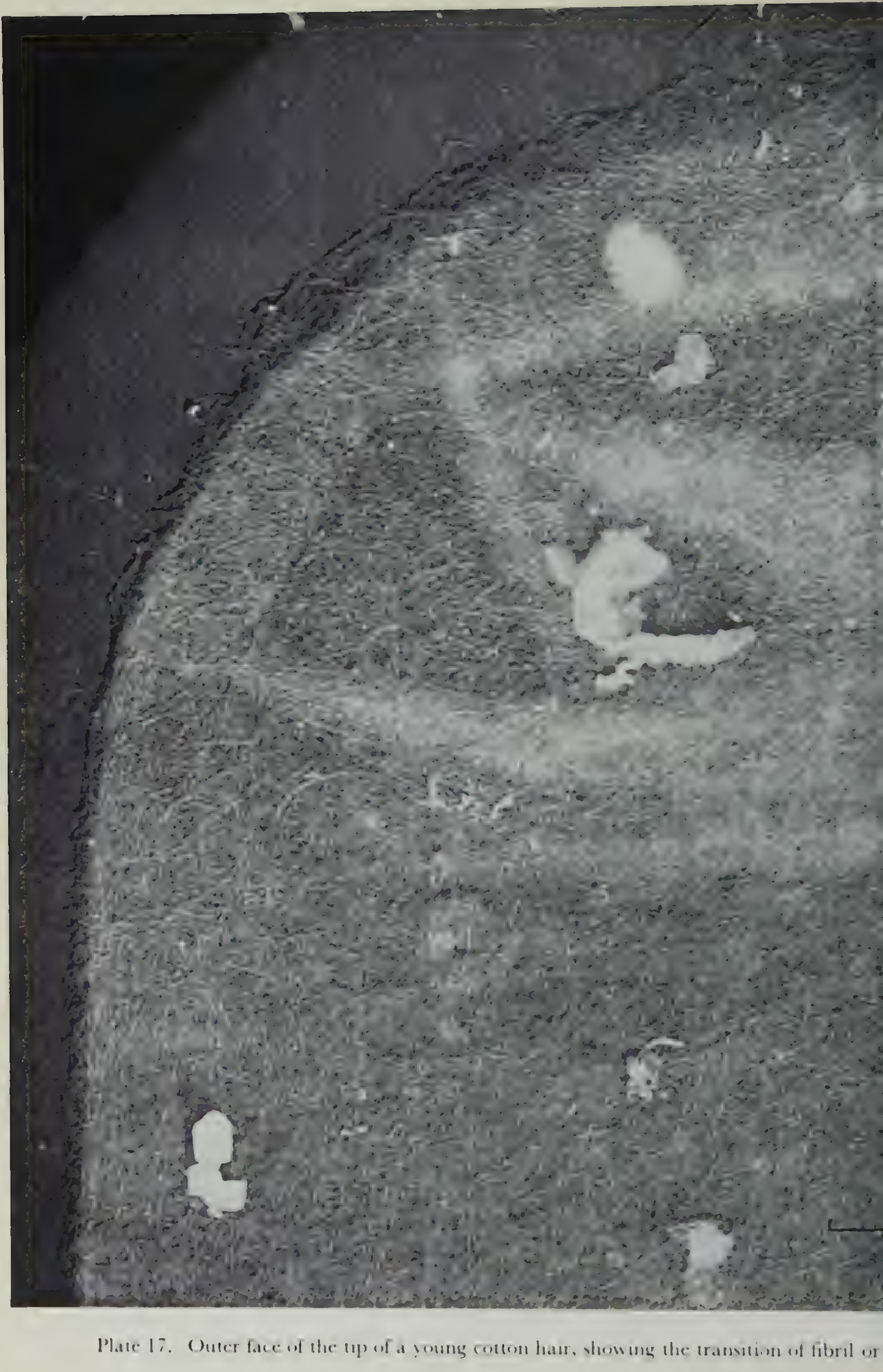
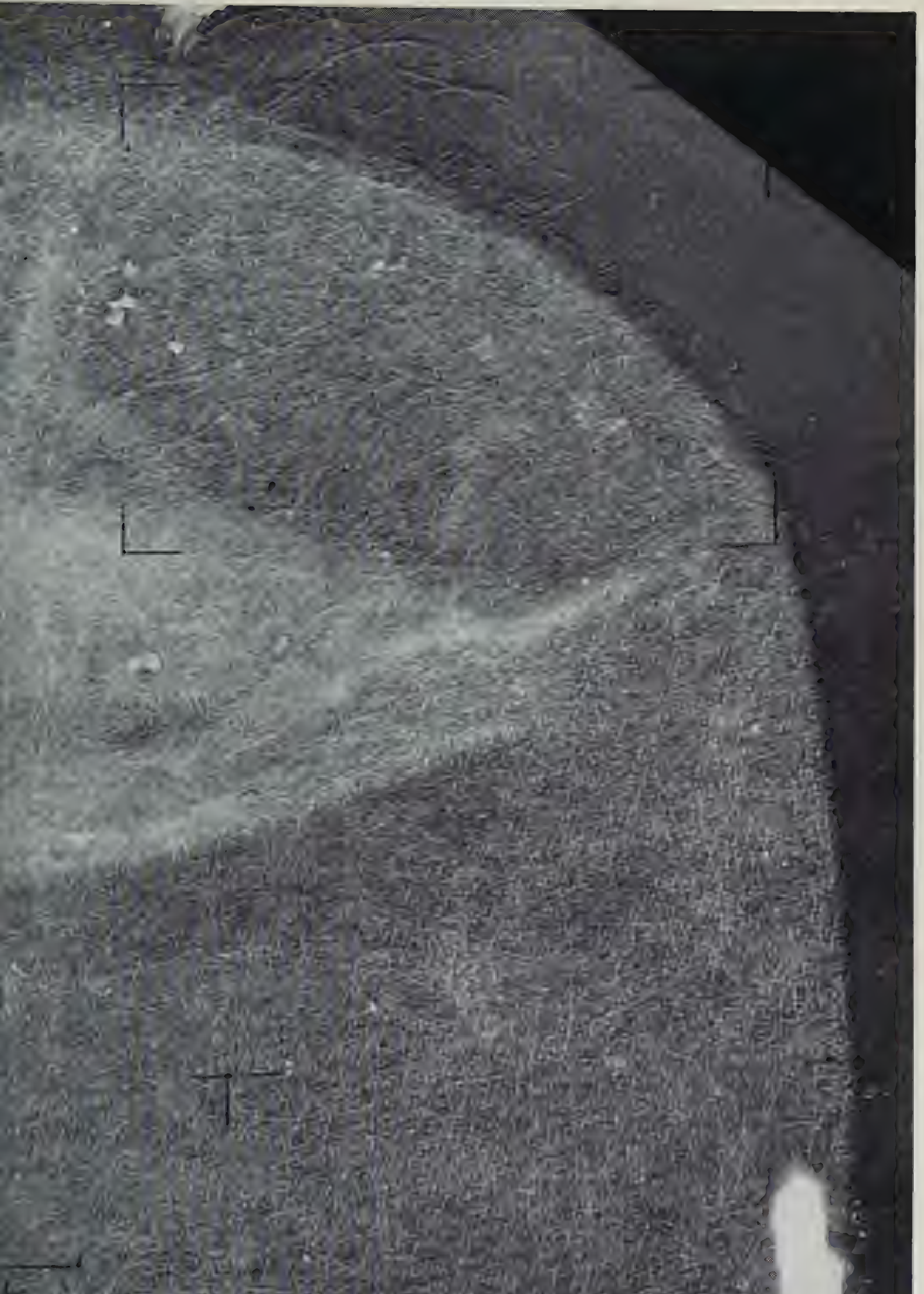


Plate 17. Outer face of the tip of a young cotton hair, showing the transition of fibril or



from isotropic at the tip to nearly axial in the cylindrical part. See also Plate 18a and b.

a lengthening growth zone. All over its length transverse fibrils will be deposited onto the inner face of the cell wall. On shifting outwards the fibrils will become isotropically and eventually, axially oriented.

In the root hairs of *Zea mays*, maybe exemplary for the root hairs of most plants growing in soil, neither birefringence nor electron microscopy indicate the presence of transverse fibrils on the inner side of the cell wall. This would indicate that the manner of growth in the tip — the tubular part of the root hair does not grow at all — is such that axial extension does not in any area prevail over transverse extension. Fig. 5, I may serve to illustrate our concept[1].

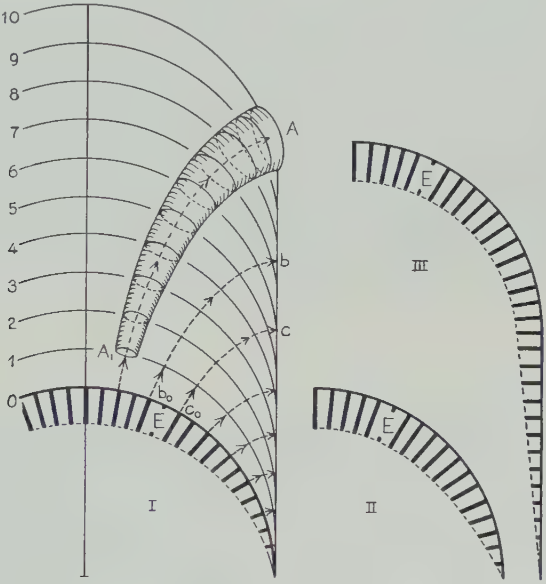


Fig. 5.

I. Schematic representation of the growth of the cell wall of a root hair.
0, 1, 2, etc. borderlines at subsequent time intervals.
b_0b, c_0c; paths of points on the cell wall.
A_1A: path and extension of an area of the cell wall.
E: graphic representation of the amount of cell wall material deposited in the unit of time per unit area onto the inner face of the cell wall.
II and III: Distribution of cell wall material leading to predominant axial extension: II different distribution of E in the tip, III additional growth in the tubular part.

The way the tip of a cell grows, is correlated with the distribution, by the cytoplasm, of cell wall materials — cellulose, pectin, hemicellulose etc. — over the inner face of the cell wall at the tip. If these substances are deposited according to the concept visualized in fig. 5 I, the primary cell wall will stay isotropic throughout. A different distribution of materials as, *e. g.*, in fig. 5 II and 5 III will lead to prevailing axial growth and this will involve deposition of transverse fibrils onto the inner side of the cell wall and reorientation of the fibrils on the outer side. *Vide* de Wolff end Houwink (14)

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[1] Compare Reinhardt, M.O. 1892 Jahrb. wiss. Bot. 23:479.

In the *Tradescantia* staminal hairs the inner layer of cellulose fibrils is transversely oriented. This would indicate that in any area axial extension of the cell wall prevailed over transverse. The outer layer, however, is not axially oriented. The latter observation proves that the prevalence of the axial extension is only slight. This makes us assume that the way these hairs grow, is intermediate between the ways root hairs on the one hand and cotton hairs on the other, do grow. Growth in this case is not confined to the tip, as it is in the root hair. The cylindrical cells of the hair, however, on elongating, also widen, and this will keep the fibrils from becoming axially oriented.

Phycomyces sporangiophores too, have an isotropic outer and a transversely oriented inner fibril layer. With young sporangiophores we may assume the cells to grow in a way intermediate between root hairs and cotton hairs. After a sporangium has been formed, however, the sporangiophore has an annular growth zone, with maximum growth slightly below the sporangium. Hence the fibrils will be transversely oriented from the start. A transverse layer has to be extended much more than an isotropic layer if it is to be turned into an axially oriented one. Moreover, in both cases the growth zone is slightly conical, widening towards its base.

If fibril reversion and hence, slipping of fibrils, happens in epidermal cell walls, in fungal hyphae and in cell walls of pith cells bordering on the intercellular space, then this is even more likely to occur in cell walls separating meristematic cells, for the latter walls are much thinner and moreover they are not cutinized. In a previous paper (13) attention was drawn to some facts pointing to the probability of multi-net-growth occuring in wood. Also the EM-graphs of cell walls of meristematic cells published by MÜHLETHALER (7) are compatible with the concept of multi-net-growth.

The Zürich school offers quite a different explanation for the architecture of these cell walls and for the growth of these cells. It involves several assumptions, *viz.*, intrusive growth of cell tips and tip perforation by the protoplasm. This would weave a new cell wall and in this way add a new tip to the cell. However, since extension of a fibrillar network has been proved to occur, our explanation of tip growth seems more likely and the possibility of symplastic growth should not be disregarded.

SUMMARY

The architecture of the extending cell walls of cotton hairs, *Juncus* stellate pith cells, and maize root hairs has been studied. The observed facts could be explained on the basis of the multi-net-growth hypothesis.

The cells investigated were found to be completely enveloped by a continuous network of cellulose fibrils. Every area of the growing part of the cell wall is extending in one or in all directions. The cellulose fibrils in the cell wall must slip past one another. The cell wall does not grow thinner since new fibrils are continuously deposited onto its inner face. In the apex of the root hair, extension is the same in every direction, so that the orientation of the fibrils does not change. In cotton hairs (the extreme tip excepted) and *Juncus* stellate cell arms, however, a change in fibril orientation has

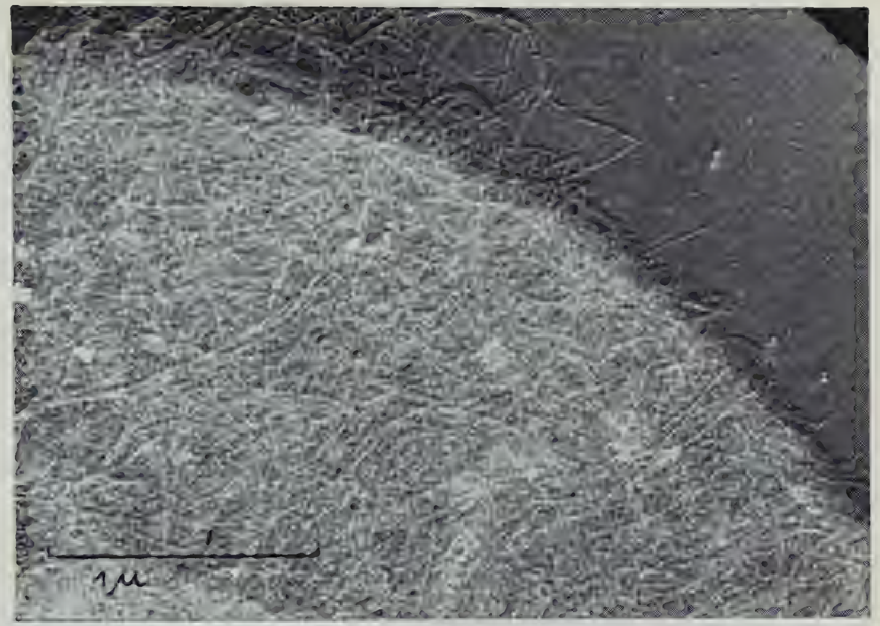

Plate 18a. Detail of plate 17, apical part.

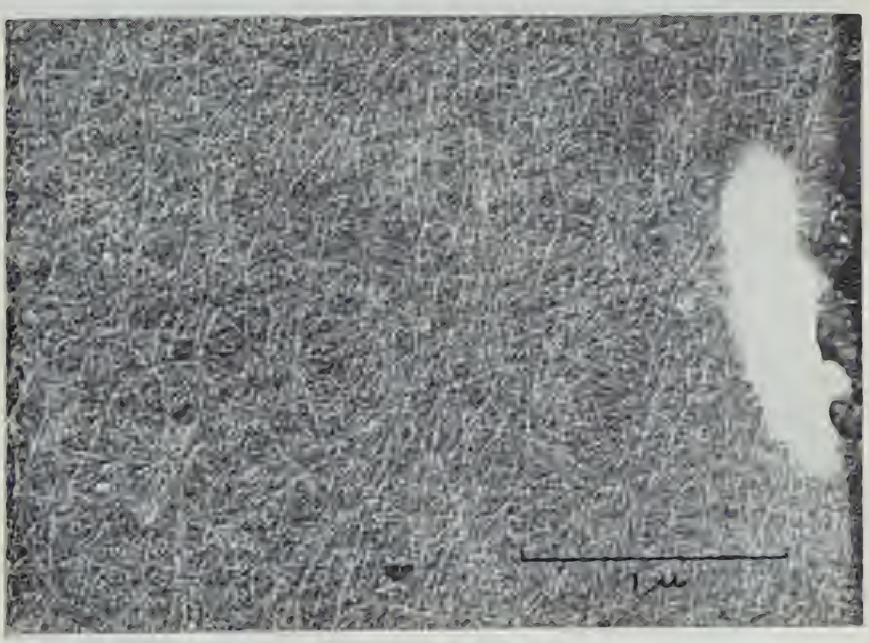

Plate 18b. Detail of plate 17, basal part.

PLATE 19

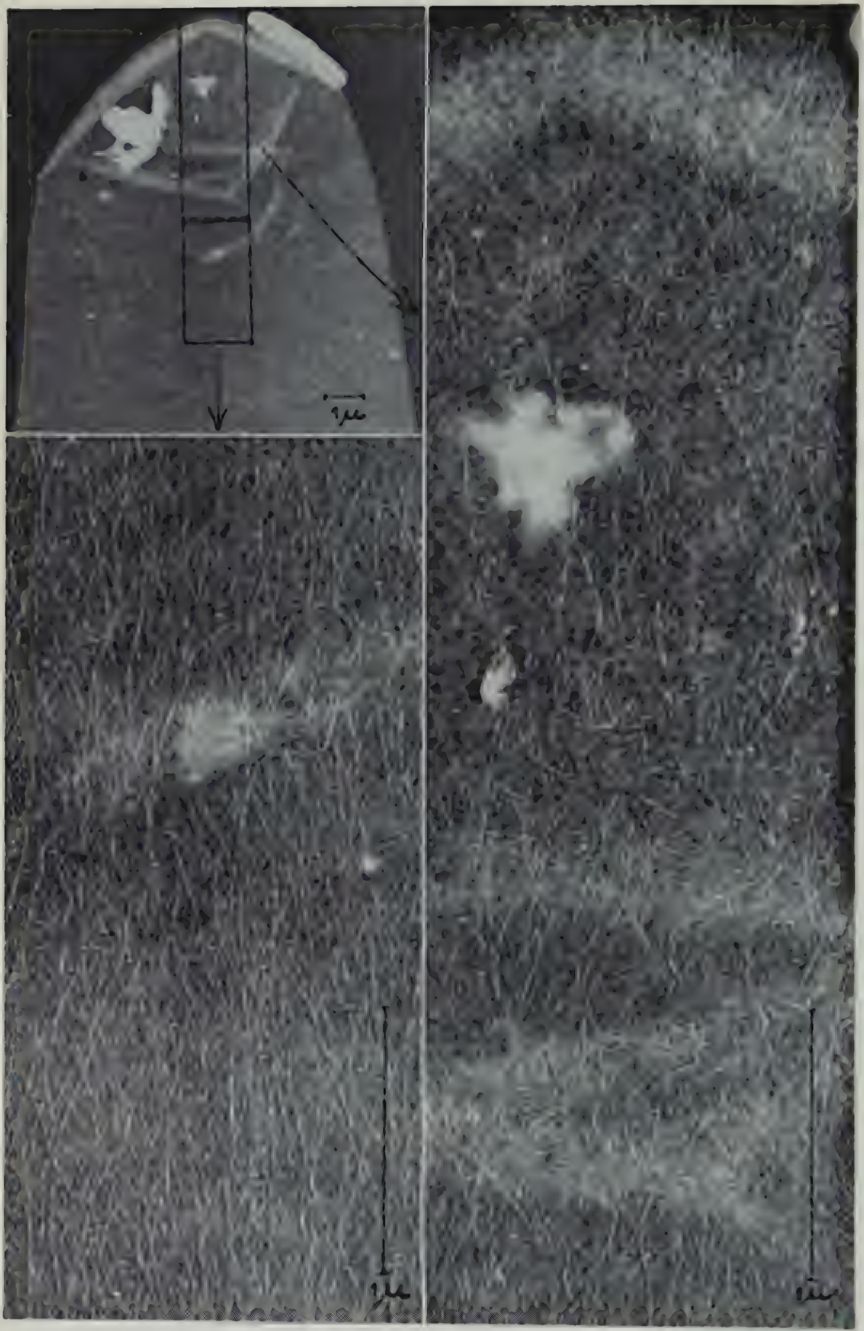

Plate 19. The tip of another young cotton hair, compare plates 17 and 18.

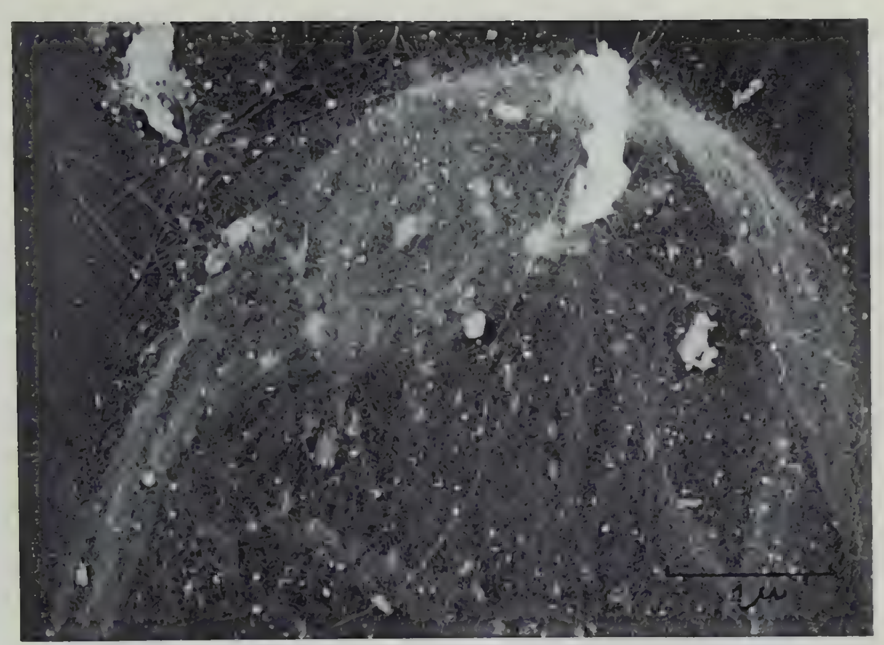

Plate 20a. *Zea mays*; Outer face of the tip of a root hair

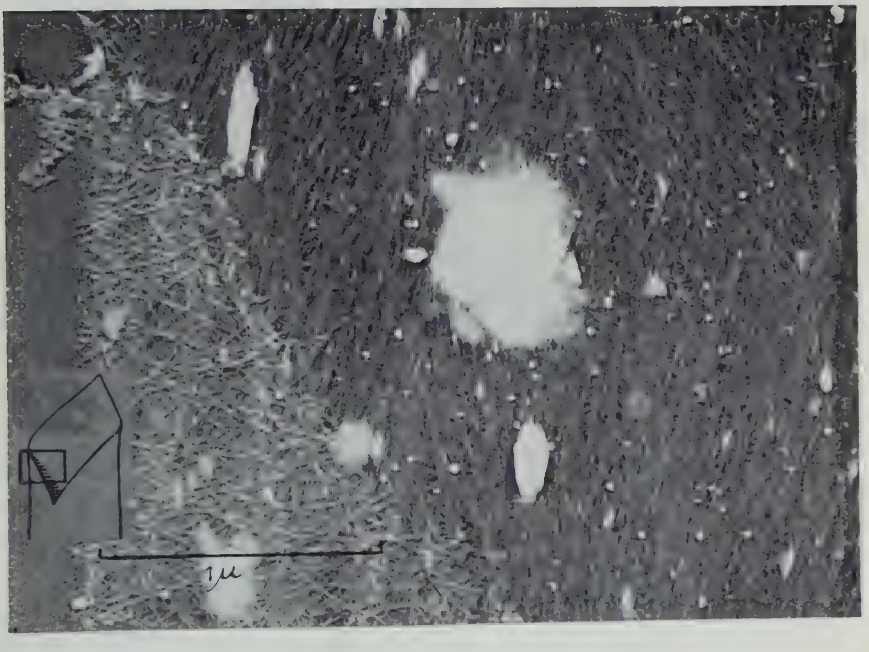

Plate 20b. *Zea mays*; obliquely cut end of a root hair, showing the isotropic outer face as well as the axially oriented inner face.

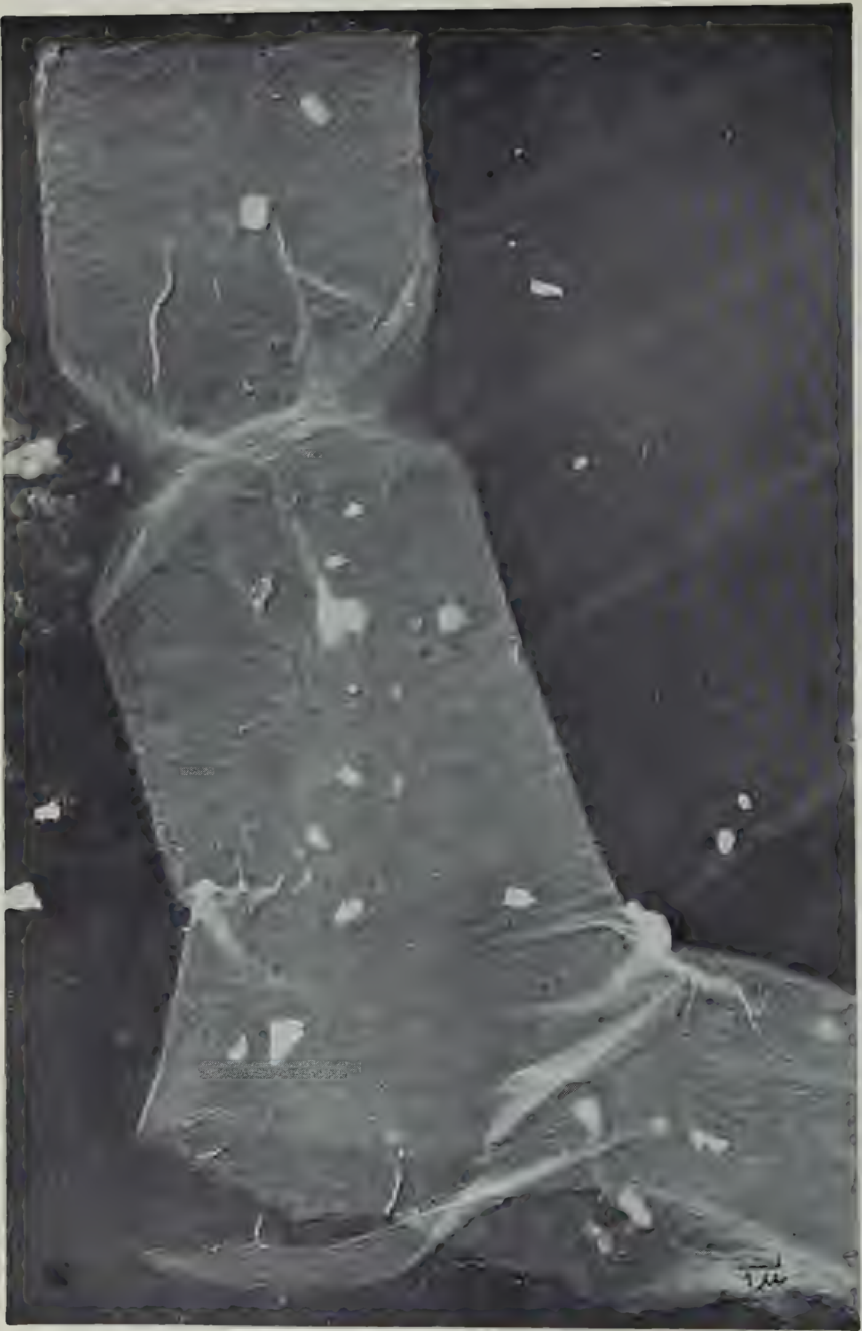

Plate 21. *Juncus effusus*: an arm of a stellate cell from the pith of a leaf base. Bottom: a portion of the central part of the cell. Top: the corresponding arm of an adjacent cell, from which it is detached.

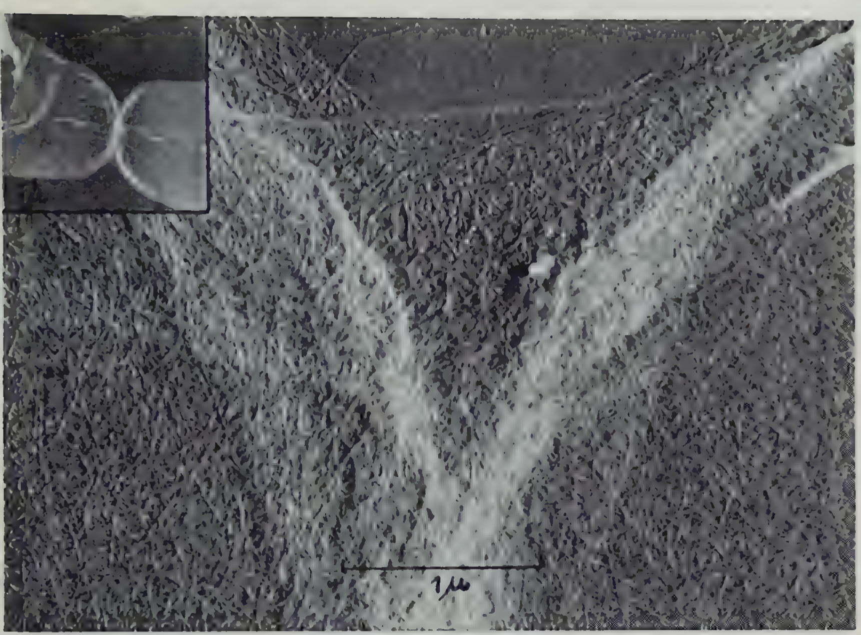

Plate 22a. *Juncus effusus*; detail of a joint of two corresponding cell arms; inset: general view. Cells at stage B.

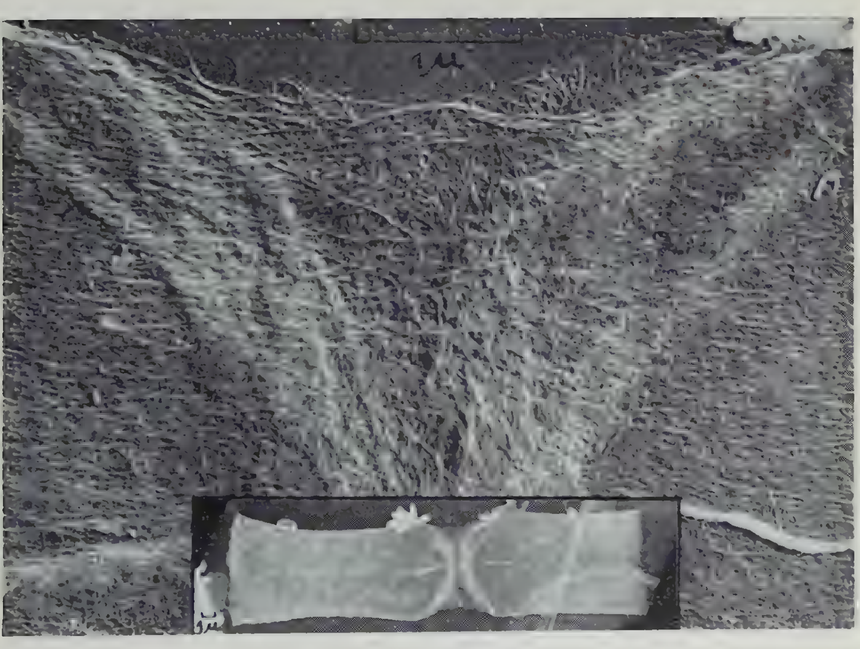

Plate 22b. *Juncus effusus*; as plate 22a. Cells at stage C.

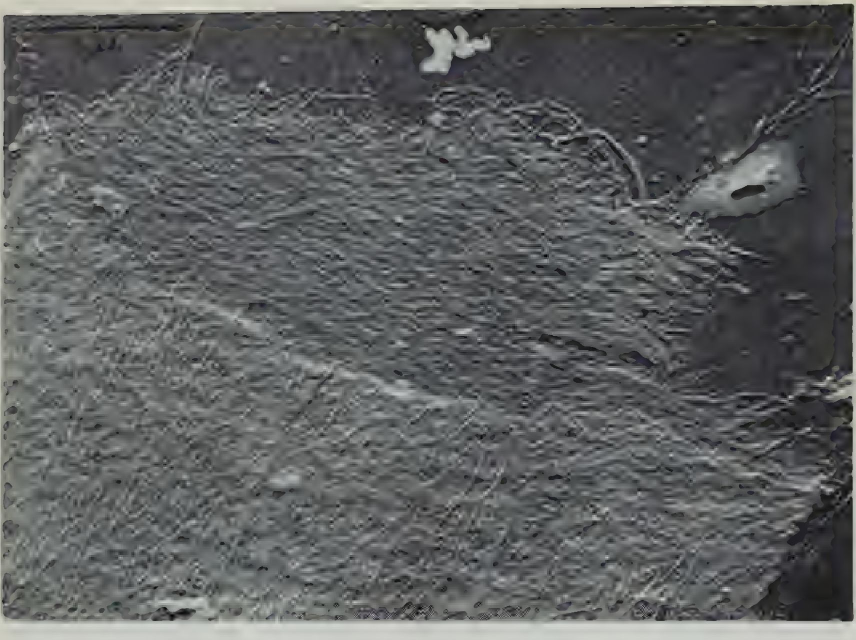

Plate 23a. *Juncus effusus*; a cell arm, cut nearly transversely. The transversely oriented inner face and the axially oriented outer face of the cell wall are shown.

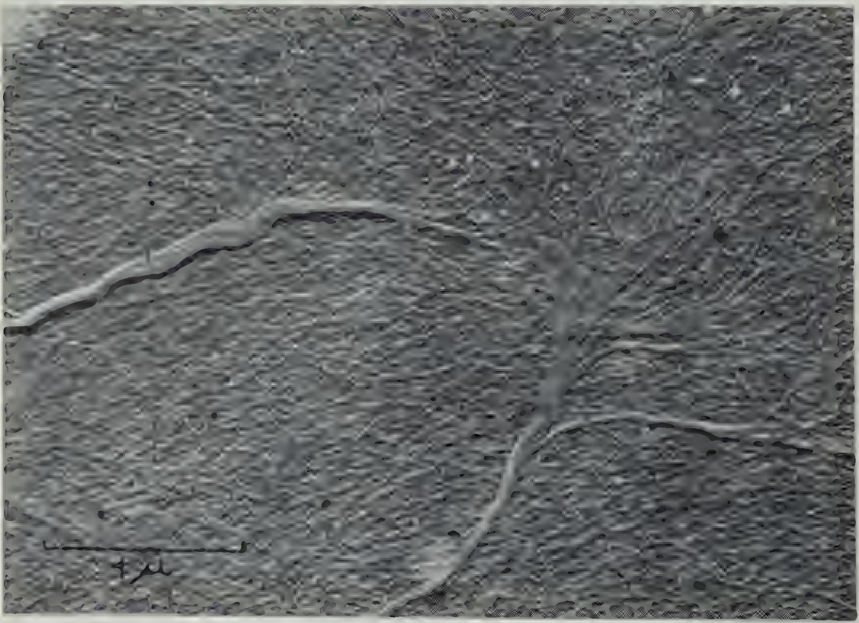

Plate 23b. *Juncus effusus*; fibril bundles found on the outside of the central part of a stellate cell. Isotropic cell wall structure.

been observed. Here axial extension prevails over transverse. This results in the orientation of the fibrils altering from the moment they are deposited until the area gets out of the growth zone.

ACKNOWLEDGEMENT

We are very much indebted to Miss L. van Dijke for the preparation of the electron microscope mounts.

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ACTA BOTANICA NEERLANDICA, Vol. 3 (3), 1954

SOME CONSIDERATIONS ON CELLULOSE FIBRIL ORIENTATION IN GROWING CELL WALLS

BY

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The following mathematical treatment demonstrates that various patterns of fibril texture in primary cell walls may be accounted for, merely by assigning appropriate — and by no means improbable — values to certain parameters.

Assume the cell wall to have axial symmetry, and assume its thickness t to be small compared with the diameter b (Fig. 1).

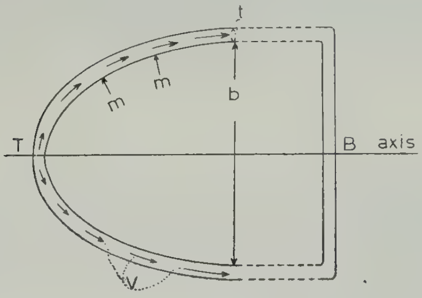

Fig. 1

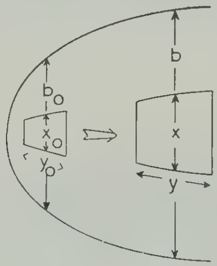

Fig. 2

The growth process is schematized as a stationary flow of incompressible cell wall material m being continuously deposited onto the inner face of the tip, and proceeding, from the moment it has been deposited, in the direction indicated by the arrows V inside the cell wall. For convenience's sake, we shall consider the tip T as fixed, so that in our picture the basal part B of the cell moves away from T with the growth velocity. Further, at any section S at a given distance from T, the cell wall material of all layers between the inner and outer face of the cell wall will be supposed to move with equal velocity, say v cm/sec.

Now, what we want to investigate, is the change in orientation of a fibril from the moment it is deposited until eventually it leaves the growth zone. Obviously this depends on the deformation of a certain volume element of cell wall material (in wich the fibril is situated), while it is shifting from the extreme tip towards the base of the growth zone (Fig. 2).

It is readily seen that dimensions in the transverse tangential direction (x) will vary as b. On the other hand, meridional dimensions (y)

within a small flowing volume element are proportional to the flow velocity v. For, since the flow is stationary, which means that the velocity at a given point is the same at any moment, two flowing points will pass through any section S with the same time interval, independent of the site of S. Hence if two points are close together, their interdistance (measured along the meridian) must remain proportional to v.

Consider a volume element with initial dimensions, diameter and velocity x_0, y_0, b_0, and v_0, then at any later stage

$$\frac{\text{transverse dimension } (x)}{\text{meridional dimension } (y)} = \frac{x_0 b}{b_0} \Bigg/ \frac{y_0 v}{v_0} = \frac{x_0 b}{y_0 b_0} \cdot \frac{v_0}{v} \qquad (1)$$

The velocity v can be expressed in more essential variables as follows: Consider the volume E of cell wall material deposited in the unit of time onto the inner face of the cell wall between T and the cross section S (Fig. 3). This volume of cell wall material has to pass through the section S also in the unit of time. Since the area of this section is πbt, we obtain for the velocity $v = E/\pi bt$. Writing the initail values of the variables with the suffix $_0$, substitution in equation (1) yields

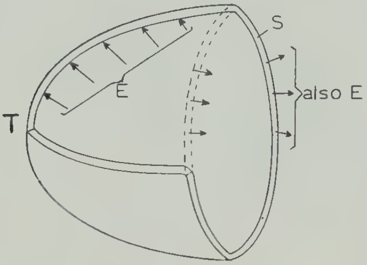

Fig. 3

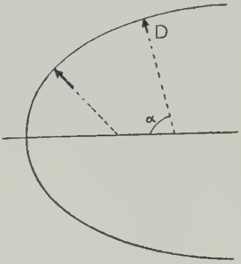

Fig. 4

$$\frac{\text{transverse dimension } (x)}{\text{meridional dimension } (y)} = \frac{x_0 b}{y_0 b_0} \cdot \frac{E_0}{\pi b_0 t_0} \Bigg/ \frac{E}{\pi bt} = \frac{x_0 E_0}{y_0 b_0^2 t_0} \cdot \frac{b^2 t}{E}$$

Now this means that the fibrils will retain their orientation throughout if b^2t/E is constant. With t constant, this will apply if the amount of cell wall material deposited between T and any section S is proportional to b^2, or, otherwise stated, if the quantities D deposited onto a unit area of the inner face of the cell wall are proportional to cos α (Fig. 4) (Compare HOUWINK and ROELOFSEN (1954), Fig. 16a. (This represents the probable way of growing of a root hair).

Obversely the change in fibril orientation observed in various plant cell walls may be explained either by a changing thickness of the cell wall ($t \neq t_0$) or by E/b^2 not having a constant value, or by both these causes. For instance, if t is constant, but E/b^2 increases from T towards the base of the growth zone, axial extension of the fibril layers will prevail (Compare HOUWINK and ROELOFSEN (1954), Fig. 16b and c). This may apply with cotton.

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ACTA BOTANICA NEERLANDICA, Vol. 3 (3), 1954

POTAMOGETON × CRASSIFOLIUS FRYER IN THE NETHERLANDS

BY

E. W. CLASON AND TH. REICHGELT

(Received Jan. 14th, 1954)

During the summer excursion of the section for investigation of the flora of the Netherlands of the Royal Netherlands Botanical Society Mr H. H. Prell was struck by the appearance of certain *Potamogeton* leaves, differing from surrounding normal floating leaves of *P. natans* L. by a brighter green colour, and by their laminae not lying quite flat on the water and being immersed in part. The plant was found July 20th, 1953 in a shallow peaty ditch on the inner side of the dike around the Zuidlaren Lake (province of Drente) at its southeastern corner.

The material collected by us agrees almost completely with the description of *P.* × *crassifolius* Fryer, Journ. of Bot. **28**: 321, tab. 299, 1890.

For the benefit of those to whom this publication is not readily accessible we quote:

"*Rootstock* with thick stolons, rooting deeply in the soil, stem 4–5 ft long, very stout, round, simple below, branched above with simple branches; *leaves all stalked, coriaceous, opaque when mature; lower leaves* reduced to submerged phyllodes, or narrowly lanceolate and tapering into the petiole, or with a distinct lanceolate lamina, *all thick and coriaceous like the upper ones;* distant, few in number, *usually all decayed by the time of flowering; upper leaves very thick and fleshy*, oblong-elliptical, or oval, with a *prominent fold at the base* of the lamina, which is slightly decurrent or rarely lanceolate and gradually narrowed into the stalk; *petiole flat above*, slightly enlarged towards the apex, *shorter than the lamina; stipules* not winged, *not channelled on the back*, but with two conspicuous green ribs, horny with scarious edges, or herbaceous, acute, lowest sometimes bearing a short phyllode, or more rarely a long lanceolate ordinary lower leaf; *peduncles of equal thickness throughout*, terminal becoming lateral by growth of the branch, equalling or slightly exceeding the stem in thickness, 2–3 times as long as the flower-spike, much shorter than the subtending leaves; *flower-spike* cylindrical, dense, 1–1$^1/_4$ in. long, usually (always?) barren, perianth-leaves closed at the time of flowering, but the stigmas exserted; *colour* of the whole plant *bright green*, or with the upper young leaves sometimes reddish or streaked with reddish purple".

Our plant (fig. 1) disagrees with this description only in its peduncles being not more than 1–2 times as long as the spike. No more than Fryer we did find any ripe fruits. The perianth segments continue to be tightly appressed to the ovaries; they are dented at the back. Even in a stem carrying as many as three flower-spikes the ovaries of the undermost of them were still undeveloped, whilst in comparable species, as far as we know, development has always started in similar specimens. This sterility strongly suggests a hybrid origin of our plant, as of Fryer's.

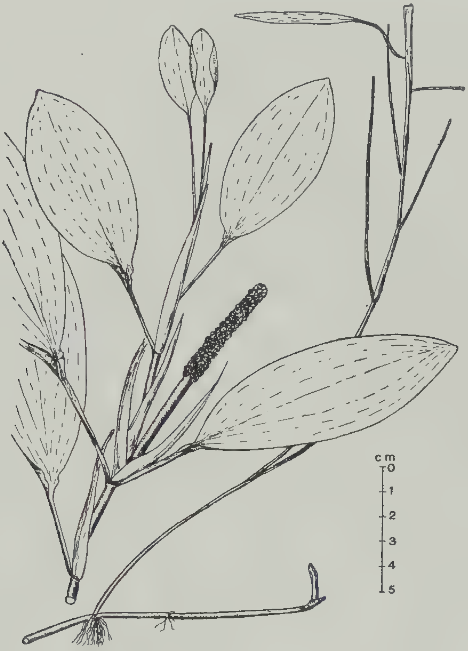

Fig. 1. Potamogeton × crassifolius Fryer. Left: flowering shoot. Right: rhizome with juvenile shoot (phyllodes).

The latter (l.c.) considers his *P.* × *crassifolius* as the result of the crossing of *P. zizii* M. et K. with *P. natans* L. Our plant was found at a distance of approximately 500 meters from a station of *P. zizii* (Clason, Act. Bot. Neerl. **1**, 491, 1953); although the two spots are now separated by a dike, this did not exist until very recently, and the whole site was formerly periodically inundated. Because *P. natans* L. (*f. prolixus* Koch) grows between the plants of *P. zizii* too, *P.* × *crassifolius* may in our case have originated from these two species as well.

The characters of *P.* × *crassifolius* are compatible with the assumption of *P. zizii* and *P. natans* entering into its parentage. The influence of *P. natans* is distinctly discernable in this interspecific hybrid in the following characters:

1. the general habit is that of *P. natans*;
2. the juvenile shoots carry phyllodes, which are no longer present in flowering shoots with floating leaves;
3. the floating leaves have distinct folds at the base, and sometimes a joint is hinted at by a slightly lighter colouring at the top of the petiole.

The plant differs from *P. natans* in:

a. the conspicuously light green colour of its leaves. These are not, however, thinly membranous, as in *P. zizii*, but as thick as those of *P. natans* (hence the specific epithet); Fryer's expression "very fleshy" is probably meant in a relative sense;
b. the lamina not being entirely flat but slightly and irregularly undulated, which results in parts of it, especially along the margins, being immersed;
c. the base in most leaves passing decurrently into the petiole, although the rounded base of *P. natans f. prolixus* does occur likewise;
d. the joints below the blades being entirely absent or only represented by a faint indication.

This last group of characters can be ascribed in our opinion to *P. zizii* influence. Of the broad-leaved *Potamogeton* species only *P. lucens* L., along with *P. natans* has been found in the vicinity (Clason l.c.); as there is nothing in our hybrid which points to *lucens* influence (e.g. thickened peduncles, cuspidate leaves) there is no reason in our opinion to consider this species as a possible parent. Moreover, the hybrid has been formed near the habitat of the rare *P. zizii*; were *P. natans* and *P. lucens* the parents, this would mean an extraordinary coincidence in view of the fact that these species are very commonly found, also in the northern part of the Netherlands, without their hybrid having recorded so far. from this region.

The present case indeed is the first on record, so far as we know, of any *Potamogeton* hybrid found in the Netherlands (cf. Kloos, Ned. Kr. Arch. **46**, 556, 1936.) Fryer (l.c.) found his *P.* × *crassifolius* in a restricted part of Cambridgeshire only, and literature has supplied us with only one instance of a plant supposed to be this hybrid, from Bavaria by Fischer (Ascherson & Graebner, Synopsis 1, ed. 2: 508, 1913).

Specimens of the hybrid are preserved in the Rijksherbarium, Leiden, the University herbarium, Groningen, and in several private collections.

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EIN NEUER, PARASITÄRER ASCOMYCET AUS SÜDAMERIKA

VON

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(Eingegangen am 26. Jan. 1954)

Beim Determinieren von Phanerogamen am botanischen Museum in Utrecht fand Herr G. VAN ARKEL auf lebenden Blättern von *Tropaeolum wagenerianum* Karst. einen parasitären Pilz, den er mir in dankenswerter Weise zur Bestimmung überliess. Es handelt sich bei ihm um einen pseudosphaerialen Pyrenomyceten, der sich nach der hier vorhandenen Literatur mit keiner bekannten Art identifizieren liess und der daher beschrieben werden soll.

Zerstreut auf der Unterseite der lebenden Blätter sind rundliche, flache, tiefschwarze Pilzräschen von 0.5–1 mm Grösse sichtbar; auf der Blattoberseite zeigen sich an den betreffenden Stellen etwas erhabene, rundliche, bis 2 mm grosse, gelbliche oder bräunliche Verfärbungszonen. Sonst bleibt das Blattgewebe unverändert. Die flachen Räschen bestehen aus zahlreichen, dicht stehenden und meist seitlich miteinander verwachsenen, rundlichen oder durch seitlichen Druck senkrecht ellipsoidischen, an den Berührungsflächen abgeplatteten Fruchtkörpern. Diese stehen oberflächlich und sind mit einem verschmälerten, senkrecht prosenchymatisch aufgebauten Hypostroma in den Epidermiszellen verankert.

Die erst völlig geschlossenen Gehäuse öffnen sich bei der Reife durch Wegbröckeln der Scheitelpartien. Die entstehende Mündung ist unregelmässig rundlich und wird mit zunehmender Reife ziemlich weit. Die Wand der Gehäuse ist vor allem oben dunkel, ziemlich dick und besteht aus derbwandigen, eckig rundlichen, durchscheinend schwarzbraunen Zellen. Nach aussen ist sie durch mehr oder weniger stark vorragende, einzelne Zellen oder kleine Zellkonglomerate feinkörnig rauh (siehe Abbildung 1). Seitlich ist die Wand dünner, hier sind die Zellen heller, dünnwandiger und konzentrisch mehr oder weniger stark niedergedrückt. Der hypostromatische Fuss besteht aus rundlich-eckigen oder in senkrechter Richtung etwas gestreckten, hellwandigen Zellen. Nach unten löst sich das Gewebe des Fusses in sich im Mesophyll der Nährpflanze verlierende, hyaline Hyphen auf.

Die Fruchtschicht wird durch mehr oder weniger zahlreiche, parallel oder etwas büschelig stehende Asci gebildet. Diese sind von erst zellig gegliederten, faserigen, später verschleimenden Paraphysoiden umgeben. Sie besitzen eine ziemlich dicke, doppelte Membran und enthalten acht zweizellige, sehr lange hyalin bleibende, sich im Alter meist erst ausserhalb der Asci gelblich färbende Sporen.

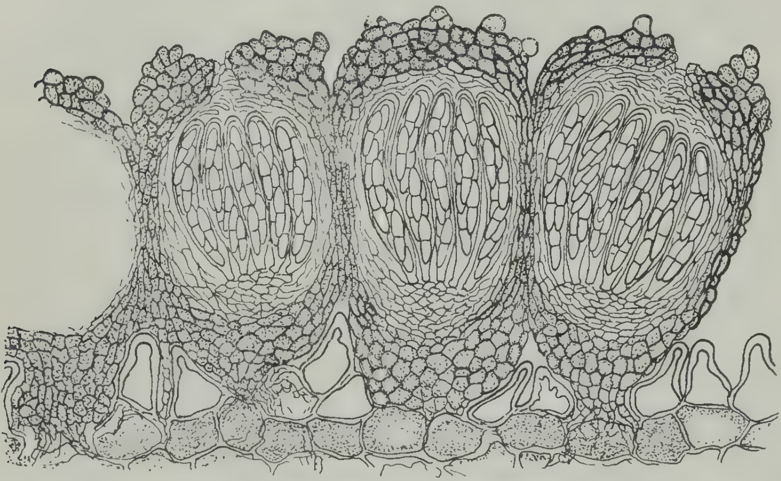

Abb. 1. Schnitt durch 3 Fruchtgehäuse von *Rosenscheldiella tropaeoli*. Die zwei seitlichen Fruchtkörper sind median, der mittlere etwas seitlich getroffen. Vergr. 350 mal

Diese Diagnose passt zu der von Theissen und Sydow (1915) aufgestellten Gattung *Rosenscheldiella*, wie diese von Hansford (1946) umgrenzt wurde. Dieser Autor hat die beiden monotypischen Gattungen *Monopus* Theiss. et Syd. (1915) und *Botryothecium* Sydow (1937) richtigerweise mit dem bisher ebenfalls monotypischen Genus *Rosenscheldiella* vereinigt. Die Gattung umfasst heute insgesamt vier Arten (vgl. Sydow 1921, Petrak, 1941), die alle auf lebenden Phanero-

Name	Wirtspflanze, Fundort	Pilzrasen	Fruchtkörper μ	Sporen μ
R. styracis (P. Henn.) Th. et Syd. . . .	*Styrax polyanthus* Perkins etc. (Brasilien, Costarica)	¼–1 mm rundlich	130–170 × 100–140	26–32 × 7–10
R. pulverulenta (B. et C.) Hansf.	*Styrax spec.* (Cuba) . .	1–1½ mm rundlich	150–170 × 120–130	21–25 × 5–6
R. orbis (Berk.) Petr.	*Litsea glauca* Siebold etc. (Ceylon, Japan) . .	¼–2 mm rundlich	60–80 × 50–75	15–20 × 4.5–6
R. ugandense (Syd.) Hansf.	*Croton macrostachys* Hochst. (Uganda) *Neoboutonia macrocalyx* Pax (Belg. Kongo)	⅓–½ mm lang 200–400μ breit	140–170 × 80–110	24–33 × 7–9.5
R. tropaeoli n. sp. . .	*Tropaeolum wagenerianum* Karst. (Bolivien)	0.5–1 mm rund	120–145 × 70–125	16–21 × 4–6

gamenblättern ohne Fleckenbildung parasitieren. Wie schon aus der folgenden Aufstellung hervorgeht, müssen sich diese Arten sehr nahe stehen; sie wurden aber auf sehr verschiedenartigen Nährpflanzen gesammelt und eine allfällige Identität könnte nur durch positive Infektionsversuche bewiesen werden. Da man die bisher bekannten Arten vorläufig als specifisch verschieden betrachten muss, ist der Pilz auf *Tropaeolum* neu zu beschreiben. Für ihm wurde folgende Diagnose entworfen:

Rosenscheldiella tropaeoli *spec.nov.*,

Maculis nullis, caespituli peritheciorum hypophylli, ambitu plerumque circulares, 0.5–1 mm diam., laxe dispersi. Perithecia densissime stipata, lateraliter plus minus connata, plerumque subglobosa vel ellipsoidea, 120–145 μ alta, 70–130 μ lata, collo plano, prima clauso, postea poro irregulariter rotundo aperto praedita. Stroma basale mox parce, mox magis evolutum, planum, epidermide leniter innatum, 30–50 μ crassum, prosenchymatice e cellulis pellucide brunneis, 6–12 μ diam. metientibus compositum.

Pariete peritheciorum molliter membranaceo, ca. 17–24 μ crasso, e cellulis angulosis pellucide atro-brunneis, 6–10 μ diam. metientibus composito, intus subito in contextum hyalinum fibroso-cellulosum transeunte, extus ob cellulas prominulas asperulo.

Asci cylindracei vel clavati, antice rotundati, membrana dubia apicali incrassata, deorsum noduloseque stipitati, 8-spori, 60–80 × 10–13 μ. Sporae oblongo-clavatae, utrinque rotundatae, antice indistincte, postice plerumque magis attenuatae, rectae, circa medium septatae, leniter constrictae, diu hyalinae, tandem flavo-brunneae, 16–21 × 4–6 μ. Paraphysoides hyalina, indistincte fibrosa constantes.

Hab. in foliis vivis Tropaeoli wageneriani Karst., Bolivia, Unduari, 3.7.1950, coll. Miss W. M. A. Brooke.

Die Gattung *Rosenscheldiella* soll nach PETRAK (1941) am nächsten mit *Phaeosphaerella* Karst. verwandt sein und sich davon vor allem durch die oberflächlich einem Hypostroma aufsitzenden und nicht dem Substrate eingesenkten Fruchtkörper unterscheiden. Nach der Typusart beurteilt fällt aber *Phaeosphaerella* mit *Venturia* de Not.-Sacc. zusammen (vgl. MÜLLER und VON ARX. 1951) *Rosenscheldiella* gehört jedoch ohne Zweifel in die Familie der *Venturiaceae* (VON ARX, 1952) und unterscheidet sich z.B. von *Phaeocryptopus* Naum. nur durch die nicht einzeln den Stomata, sondern herdenweise den Epidermiszellen eingewachsenen und gewöhnlich miteinander verbundenen Fruchtkörper. *Gibbera* Fr. ist vor allem durch ein grösseres, oft mehrere Gehäuse tragendes Hypostroma oder duch grössere, meist nicht in dichten Rasen stehende und nicht miteinander verwachsene Fruchtkörper, sowie durch die gewöhnlich bereits innerhalb der Asci gefärbten Sporen verschieden. *Gibbera conferta* (Fr.) Petr. stellt in mancher Hinsicht eine Uebergangsform zwischen den beiden Gattungen dar. Sollten noch mehr derartige Zwischenformen gefunden werden, dann müsste *Rosenscheldiella* mit *Gibbera* vereinigt werden.

Bei ihrer Bearbeitung der *Dothideales* wurde *Rosenscheldiella* von Theissen und Sydow (1915) neben *Licopolia* Sacc. et Syd. gestellt. Diese Gattungen sollten sich nur durch die Farbe der Sporen unterscheiden, die bei *Rosenscheldiella* hyalin, bei *Licopolia* braun sein sollen. Nun werden aber bei *Rosenscheldiella* die Sporen mit zunehmender Reife ebenfalls bräunlich und diese Gattung wäre daher von *Licopolia* nicht verschieden.

Licopolia ist aber eine unsichere Gattung. Die einzige Art *L. franciscana* Sacc. et Syd. scheint bisher nicht wiedergefunden zu sein. Ein im Herbarium der Botanischen Abteilung des Naturhistorischen Reichsmuseums in Stockholm aubewahrtes Originalexemplar bestand aus einem einzigen, in abgestorbenem Zustande gesammelten Blatt. Darauf, konnten einige Fruchtkörper eines saprophytisch wachsenden Konidienpilzes gefunden werden, hingegen nicht ein der Beschreibung von *Licopolia* entsprechender Ascomycet.

Licopolia liess sich daher nicht aufklären und ist eine hinsichtlich ihrer systematischen Stellung unsichere und unzulänglich beschriebene Gattung. (Die von von Höhnel (1911) und von Theissen und Sydow (1915) gegebenen Diagnosen weichen stark voneinander ab.) Von *Rosenscheldiella* ist sie jedenfalls durch die saprophytische Lebensweise ihres einzigen Vertreters, sowie durch die sich frühzeitig braun färbenden Sporen verschieden. Wie *Xenomeris* Syd. lässt sie sich wahrscheinlich nicht von *Gibbera* Fr. trennen.

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NOVITATES VOCHYSIACEARUM I

BY

F. A. STAFLEU

Utrecht

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1. **Vochysia cassiquiarensis** Stafl. nov. spec. (fig. 1*a* and *b*)

Sectio *Ciliantha* Stafl., subsectio *Ferrugineae* Warm. A *V. vismiifolia* Spruce ex Warm. stipulis nullis, foliis longe petiolatis majoribus latioribus, nervis lateralibus pluribus, floribus minoribus calcare inflato instructis differt.

Arbor. Ramuli juveniles, petioli, inflorescentia, foliorum pagina inferior indumento ferrugineo-canescente instructi. Stipulae nullae. Folia opposita, petiolo c. 15 mm longo, lamina elliptica, c. 12–16 cm longa, c. 5½–7 cm lata, apice breviter obtuse apiculata, retusa, basi obtusa, nervis supra haud prominentibus, lateralibus subtus prominentibus, majoribus utrinque 15–20 sub angulo c. 50–60′ e costa ortis a nervo limbali undulato margini proximo junctis, venulis supra haud conspicuis, subtus prominulis, reticulatis. Inflorescentia cylindrica, densiflora, cincinnis bifloris, pedunculis 2–3 mm longis, pedicellis 5–7 mm longis, alabastris c. 7 mm longis, 1½ mm latis, subrecurvis, obtusis, calcare c. 5 mm longo, basi constricto, inflato, sub angulo 60–90′ e pedicello orto instructis. Petala suboblonga, apice obtusa; intermedium c. 5 mm longum, extus dense pilosum; lateralia c. 4 mm longa, stamen subpilosum, anthera c. 4 mm longa apice rotundata, filamento c. 2 mm longo. Staminodia c. 1 mm longa ciliata. Stylus glaber, stigmate laterali parvo instructus.

Holotypus: R. de L. Fróes 21503 in K. Brazil, Amazonas, San José do Cassiquiare, fl. 12–12–1945.

2. **Vochysia elegans** Stafl. nov. spec. (fig. 1*c* and *d*)

Sectio *Ciliantha* Stafl., subsectio *Ferrugineae* Warm. A *V. vismiifolia* Spruce ex Warm. foliis longe petiolatis, longe acuto-acuminatis, nervis lateralibus tenuibus prominulis differt.

Arbor. Ramuli juveniles, petioli, foliorum pagina inferior indumento sericeo-ferrugineo evanescente instructi. Stipulae deciduae, parvae. Folia opposita, petiolo c. 2½–3 cm longo, lamina elliptica, c. 10–12 cm longa, c. 3½–5 cm lata, basi obtusa, apice longe acuminata, acumine angusto acuto c. 15 mm longo; costa subtus prominente,

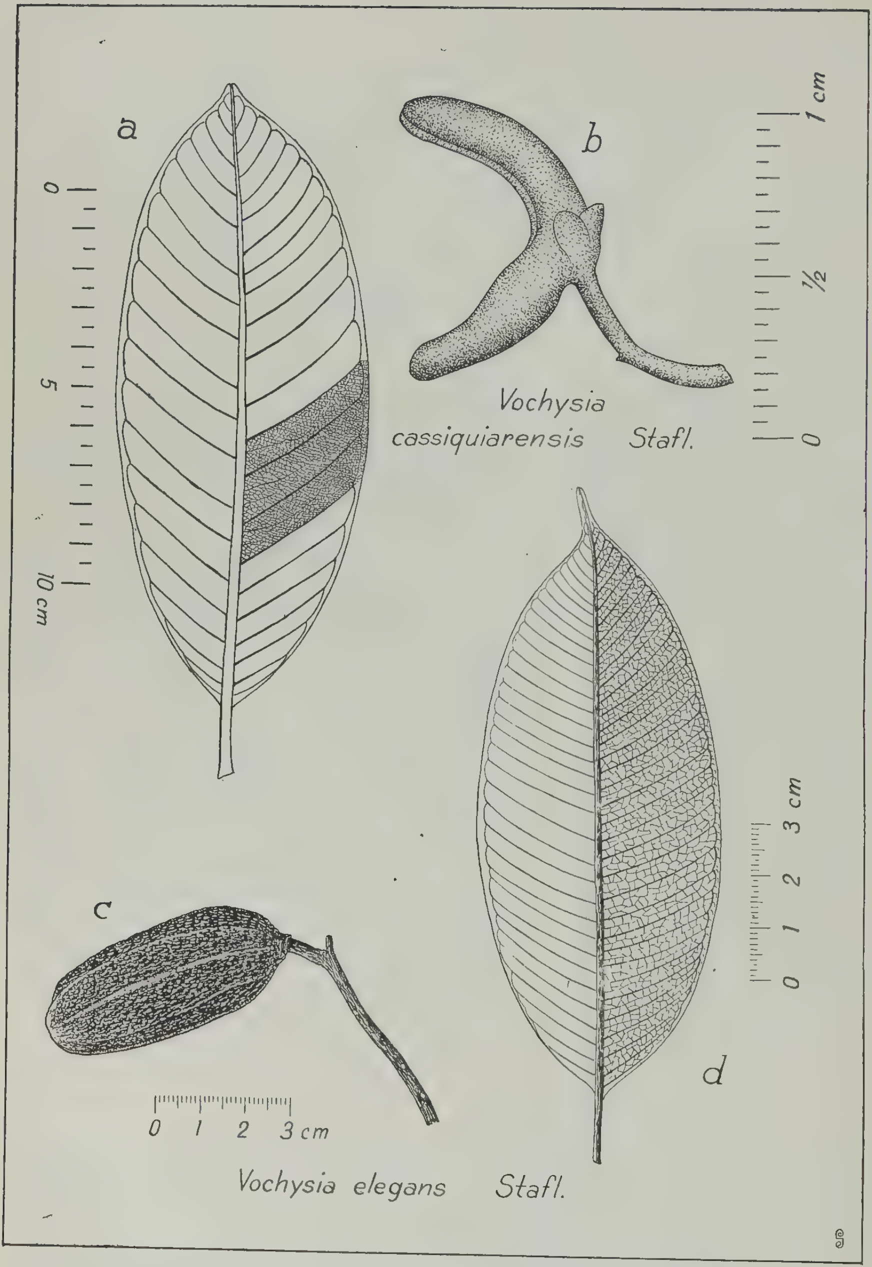

Fig. 1. *Vochysia cassiquiarensis* Stafl. *a.* leaf, *b.* flower-bud; *Vochysia elegans* Stafl. *c.* fruit, *d.* leaf

nervis lateralibus utrinque ultra 20, in utraque pagina leviter prominentibus, tenuibus, sub angulo c. 60′ e costa ortis a nervo limbali tenui undulato margini proximo junctis; venulis subconspicuis, reticulatis, supra prominulis, subtus haud prominentibus, margine haud revoluto. Capsula oblonga, c. 6 cm longa, 2–2½ cm lata, valvis oblongis nigris, rugulosis, glabris.

Holotypus: A. Ducke RB 34656 in U. Brazil, Amazonas, Uarurá, Rio Negro, acima de Uananacá, fr. 3–3–1936 (RB, U).

3. **Vochysia megalophylla** Stafl. nov. spec. (fig. 2*a* and *b*)

Vochysia e sectione *Ciliantha* Stafl. ramulis quadrangulatis, stipulis persistentibus, acutis, satis magnis, foliis glabris, oppositis, magnis, nervis haud prominentibus instructis, nervo limbali carantibus, fructibus satis magnis, verruculosis, glabris noscenda.

Arbor satis magna. Ramuli juveniles subquadrangulares, parce ferrugineo-pilosi, demum subteretes, glabri, haud decorticantes, gemmis ovatis, acutis, dense ferrugineo-pubescentibus, c. 4 mm longis. Stipulae persistentes, triangulares, acutae, c. 2–3 mm longae, basi 1–1½ mm latae. Folia opposita, glabra, petiolo c. 1½–2 cm longo, lamina elliptica vel suboblonga ad 20 cm longa et 8½ cm lata, basi in petiolum abrupte attenuata, apice breviter obtuse-acuminata; costa subtus prominente, nervis lateralibus majoribus utrinque 10–14, supra haud prominentibus et vix conspicuis, subtus parcissime prominentibus, sub angulo c. 80′ e costa ortis, prope marginem curvatis, in reticulo venularum excurrentibus, haud nervo limbali junctis. Capsula oblonga, glabra, c. 4 cm longa, 1½–2 cm lata, valvis ellipticis, fuscis, dense verruculosis.

Holotypus: E. P. Killip & A. C. Smith 15276 in NY. Colombia, Dept. Santander: Mesa de los Santos, 1500 m., dense woods, tree 25–30 ft. infl. drooping; fr. 11/15–12–1926.

4. **Vochysia laxiflora** Stafl. nov. spec. (fig. 2*c* and *d*)

Sectio *Cilantha* Stafl., subsectio *Ferrugineae* Warm. A *V. lomatophylla* Standl. stipulis magnis, acuminatis, petiolis brevibus, laminis minoribus, nervis lateralibus paucioribus, inflorescentia laxiflora, alabastris calcare incurvo instructis, stylis stigmate terminali munitis differt.

Arbor media vel magna. Ramuli juveniles, petioli, stipulae, costa foliorum indumento ferrugineo, valde canescente, demum evanescente instructi. Stipulae triangulares, acuminatae, 4–6 mm longae. Folia quaternata, petiolo c. 3–5 mm longo, lamina spatulata, c. 11–16 cm longa, c. 4–5½ cm lata, apice obtusa vel rotundata, nonnunquam emarginata, basi sensim in petiolum attenuata sed ad basin extrema rotundata; nervis supra haud prominentibus, lateralibus subtus fortiter prominentibus, majoribus utrinque 10–12 sub angulo c. 50′ e costa ortis a nervo limbali undulato margini proximo junctis, venulis supra haud conspicuis, subtus prominulis, reticulatis. Inflorescentia laxiflora, cincinnis trifloris, pedunculis c. 5–8 mm longis, pedicellis

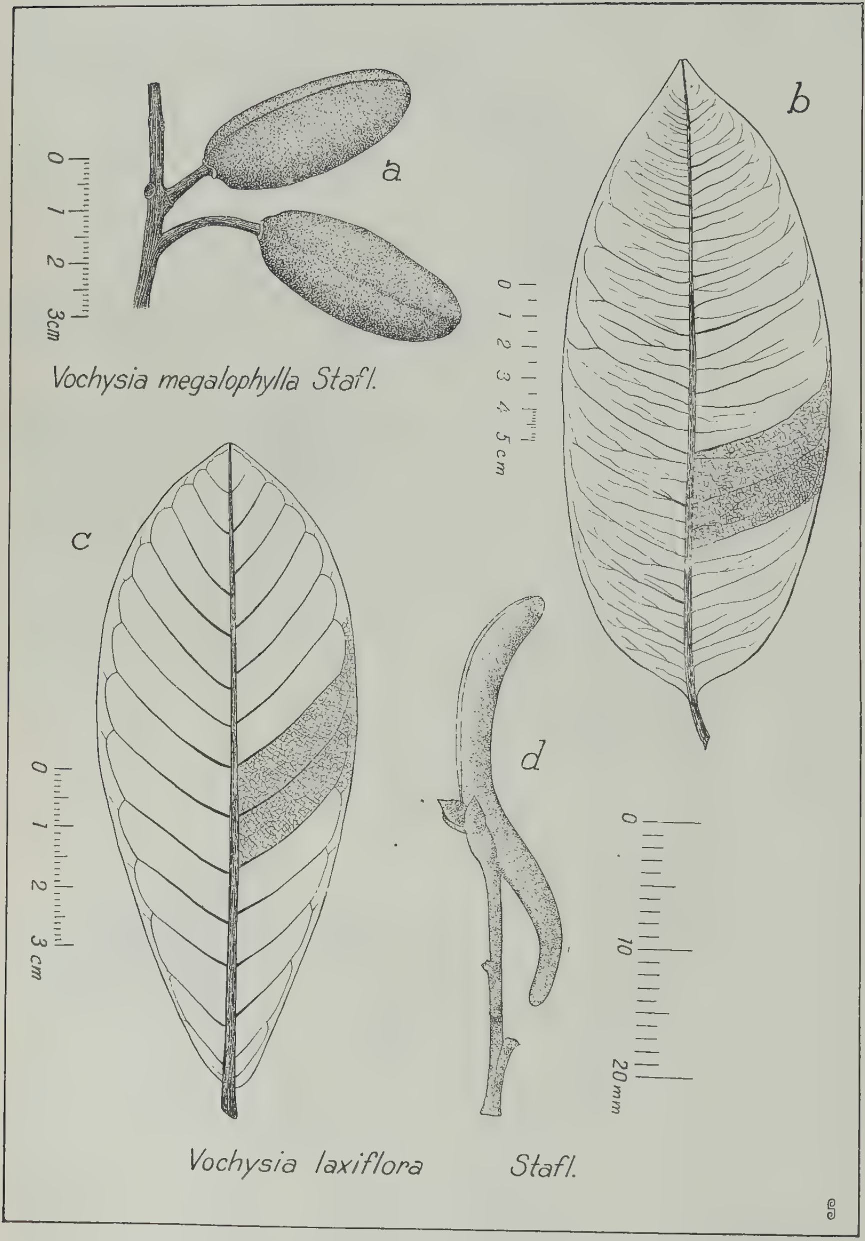

Fig. 2. *Vochysia megalophylla* Stafl. *a.* fruits, *b.* leaf. *Vochysia laxiflora* Stafl. *c.* leaf, *d.* flower-bud

c. 5–6 mm longis, alabastris ad 13 mm longis parum recurvis obtusis, calcare incurvo c. 6–8 mm longo sub angulo 0–30′ e pedicello orto instructis. Petala spatulata; intermedium c. 12–13 mm longum, apice ciliatum, dorso parum pilosum; lateralia modice breviora. Stamen pilosum, anthera c. 8 mm longa, apice rotundata, filamento c. 3 mm longo. Staminodia c. 1–2 mm longa, pilosa. Stylus glaber, stigmate terminali parvo instructus.

Holotypus: H. García-Barriga 13841 in US. COLOMBIA, Amazonas – Vaupés: Rio Apaporis entre los rios Kanana y Pacoa, 250 m. fl 1/15–12–1951: H. García-Barriga 13841 (COL,US), 13905 (COL, US), 14050 (COL, US).

5. **Vochysia cipoana** Stafl. nov. spec. (fig. 3*a* and *b*)

Sectio *Cilantha* Stafl., subsectio *Lutescentes* Warm. A *V. martiana* Stafl. *V. rotundifolia* Mart. et *V. pygmaea* Bongard stipulis persistentibus, caule robustiore, foliis majoribus late ellipticis, venulis supra conspicuis differt.

Suffrutex glaberrimus, c. 2 m altus, caule tereti paulum glauco-pruinoso. Stipulae persistentes triangulares, acutae, c. 1½ mm longae. Folia ternata, petiolo c. 1–2 mm longo, lamina rigide coriacea, late elliptica vel ovato-elliptica, 6–9 cm longa, 3–6½ cm lata, supra lucida, apice rotundata nonnunquam emarginata, basi truncata vel subcordata; nervis reticulatis, prominulis, in utraque pagina conspicuis, lateralibus anastomosentibus, haud a nervo limbali junctis. Inflorescentia subcylindrica, cincinnis 2- vel 3-floris, pedunculis 8–10 mm longis, pedicellis 8–15 mm longis, alabastris subrecurvis, obtusis, c. 18–20 mm longis, 2–3 mm latis, calcare c. 7–9 mm longo incurvo subcylindrico instructis. Petala lineari-oblonga, apice subciliata excepta glabra; intermedium stamen aequans; lateralia dimidio minora. Stamen glabrum sed margine ciliatum, filamento 3–4 mm longo. Staminodia 1–2 mm longa. Stigma terminale, diam. ½–1 mm.

Holotypus: A. P. Duarte 2626 (= RB 70087) in U. BRAZIL, Minas Geraes, Serra do Cipo, km. 135, on rocky soil, 1250m., fl. 21–4–1949 (RB, U).

6. **Vochysia obovata** Stafl. nov. spec. (fig. 3*c* and *d*)

Sectio *Cilantha* Stafl., subsectio *Lutescentes* Warm. A *V. cipoana* Stafl. foliis petiolatis, obovatis, apice rotundatis et emarginatis, pedicellis longis, alabastris longis gracilibus, calcare recto instructis differt.

Suffrutex glaberrimus, ramulis teretibus. Stipulae persistentes, parvae, acutae, ½–1 mm longae. Folia ternata, petiolo c. 8–15 mm longo, lamina obovata, 5–8 cm longa, 4½–5½ cm lata, apice late rotundata, emarginata, basi cuneata; nervis haud prominentibus, lateralibus utrinque 8–12 a nervo limbali margini proximo undulato junctis; venulis praesertim subtus conspicue reticulatis. Inflorescentia subcylindrica, cincinnis 2- vel 3-floris, pedunculis 7–15 mm longis, pedicellis 15–20 mm longis, alabastris subrecurvis, obtusis, gracilibus, c. 18–23 mm longis, 2–3 mm latis, calcare c. 7–9 mm longo, recto,

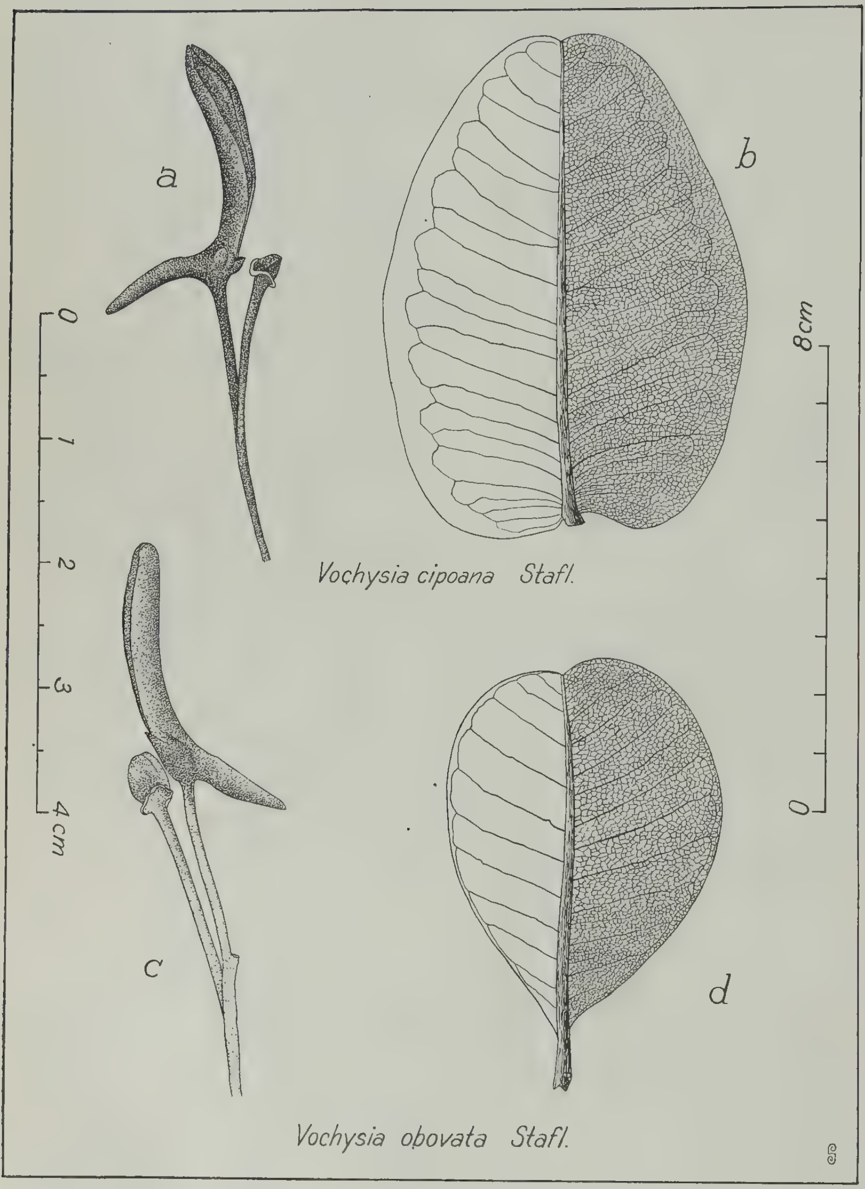

Fig. 3. *Vochysia cipoana* Stafl. *a*. flower-bud, *b*. leaf. *Vochysia obovata* Stafl. *c*. flower-bud, *d*. leaf

haud inflato instructis. Petala suboblonga; intermedium c. 20 mm longum. Stamen obtusum, c. 20 mm longum.

Holotypus: R. de L. Fróes 20139 in NY. BRAZIL, Minas Geraes, regiao de Sincorá formaçao do Rio Paraguassû (Ibiquara, Mucugê), fl. 24–2–1942.

7. **Vochysia densissima** Pilger, Notizbl. Berlin 11: 298. 1931; Macbride, Field Mus. Bot. 13(3): 884. 1950. *Vochysia vismiifolia* Spruce ex Warm. var. *densissima* (Pilger) Stafleu, Med. Bot. Mus. Utr. 95: 498. 1948.

Petioles 1–1½ cm long; leaves opposite, coriaceous, long-elliptic, 10–11 × 2–4 cm, ferrugineous-tomentellous below, long-(c. 6–10 mm) acuminate; lateral nerves c. 25 on either side, strongly prominent below; inflorescence many-flowered, cylindrical, peduncles and pedicels 2–3 mm long, spur subconical, slightly recurved, about as long as the bud (c. 6 mm), the fourth calyx-lobe strongly recurved.

Lectotypus: Tessmann 4632 in NY. This specimen agrees in all respects with Pilger's description and with the photograph (in GH) of the destroyed Berlin holotype (Tessmann same number).

8. **Vochysia majuscula** Pilger, Notizbl. Berlin 11: 297. 1931; Stafleu l.c. 95: 521. 1948; Macbride l.c. 13(3): 889. 1950.

Lectotypus: Tessmann 4797 in NY. This specimen agrees with Pilger's description and with the photograph (in F) of the destroyed Berlin holotype (Tessmann same number).

9. **Vochysia pacifica** Cuatrecasas, Rev. Acad. Colomb. 6: 548. 1946; Stafleu l.c. 95: 479. 1948.

Holotypus: Cuatrecasas 17468 in VALLE, isotypes in F and U.

10. **Qualea calantha** Pilger, Notizbl. Berlin 11: 297. 1931; Stafleu l.c. 116: 178. 1953.

Lectotypus: Tessmann 4855 in NY. This specimen agrees with Pilger's description and with the photograph (in GH) of the destroyed Berlin holotype (Tessmann same number).

11. **Qualea gracilior** Pilger, Notizbl. Berlin 11: 296. 1931; Macbride l.c. 13(3): 877. 1950; Stafleu l.c. 116: 186. 1953. *Qualea lancifolia* Ducke, Arch. Inst. Biol. Veg. 2: 53. 1953.

Lectotypus: Tessmann 4465 in NY. This specimen agrees with Pilger's description and with the photo graph (in GH and F) of the destroyed Berlin holotype (Tessmann same number).

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NEW DUTCH MARINE ALGAE I

BY

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A considerable number of algae which had not been recorded earlier from the Dutch coast, have been collected during the last years. Partly these finds have been published already by Veldkamp (1950), Koster (1952) and Den Hartog (1953). In this paper I will deal with some other interesting marine algae, eight Phaeophyceae and two Rhodophyceae.

Remarkable enough, all new finds thus far published, turned out to be large or medium-sized species. In this paper the majority of the algae mentioned are medium-sized; only 3 microscopical algae are recorded. Van Goor (1923) gives in his Algal flora only 20 microscopical species of which there are 14 native of our coast. From this we may infer that under this category many acquisitions to our flora still are to be expected.

I am much indebted to Dr J. Th. Koster for her valuable advice. Further I am grateful to A. F. Mulder for allowing me to record some of his observations.

Ectocarpus confervoides (Roth.) Le Jol. **f. pygmaea** (Aresch.) Kjellm.

The author found this form in July 1952 in a very dense, matted growth on the stipes of *Laminaria digitata* near Den Helder. The alga was also observed on the laminae, although in much smaller quantities. The Dutch specimens agree very well with the descriptions, given by Børgesen (1903), Jonsson (1903) and Lund (1941).

The form is widely distributed in the northern Atlantic. Records from the American Pacific coast are also known.

Giffordia mitchellae (Harvey) Hamel

Synonyms: *Ectocarpus mitchellae* Harvey, *Ectocarpus virescens* Thuret.

Hitherto this alga has only been found on drifting objects, washed ashore on our coast (Lucas, 1950). However, it is a native of the Dutch waters too. In October 1951 the species was collected by Mulder and the author on *Codium fragile* in the oysterbasins of Yerseke, Island of Zuid-Beveland, and on stones in the *Fucus serratus*-belt at Gorishoek, Island of Tholen.

Giffordia mitchellae occurs along the Atlantic coast of France, the British coast of the Channel and in the Mediterranean. Further it has been recorded from California and the Caribbean Sea. The Dutch localities are the northernmost known to the author.

Giffordia sandriana (Zanard.) Hamel

Synonyms: *Ectocarpus sandrianus* Zanard., *Ectocarpus elegans* Thuret. This species, which was known in Holland from drifting objects only, was collected by MULDER and the author in the Zuid-Bevelands Kanaal, in October 1951. It grew as an epiphyte on other algae, especially on *Dasya pedicellata*. In the Rijksherbarium there is another specimen, which had been collected in September 1941 by BRAKMAN in the Kanaal door Walcheren on stones in shallow water. The alga is known from the Atlantic coast from France up to the Danish waters and the Swedish West coast. It occurs also along the Scotch coast (BØRGESEN and JONSSON, 1908) and in the Mediterranean.

Ulonema rhizophorum Foslie

FOSLIE (1894) as well as HAMEL (1935) and NEWTON (1931) record this little alga as an epiphytic species on the fronds of *Dumontia incrassata*. As the last mentioned species is common in spring near Den Helder in small, littoral pools, in April 1952 a great many specimens were collected and checked on the presence of *Ulonema*, without any result however. In May of the same year the writer was more successful in collecting in the same locality a great number of *Dumontia* infected by *Ulonema* which formed little round brownish spots with a diameter of 1 to 3 mm. Also in June the species was common. It disappeared in July, together with the host. The specimens studied in May bore unilocular sporangia, originating from the basalcells of the erect filaments. The plurilocular sporangia, unknown to FOSLIE, but pictured by HAMEL and NEWTON, lacked in the Dutch material.

Ulonema rhizophorum probably is a widely distributed species which is known from Great Britain, France and Norway. In the Netherlands it is presumably not limited to Den Helder.

Giraudia sphacelarioides Derbès et Solier

This little alga, unknown from the Dutch waters up to the present, was collected twice on the seadike of Den Helder in June 1950. In both cases they were young specimens growing on the shells of living *Littorina obtusata*, and covering them with a dense brown layer.

Giraudia sphacelarioides is a Mediterranean-Atlantic species, reaching its northern limit at the Norwegian west coast (LEVRING, 1937). According to HAMEL (1937), it is fairly rare in the Channel. Also in the Dutch waters it must be considered a very rare species.

Petalonia zosterifolia (Reinke) Hamel

Although this alga is recorded in this paper for the first time it is by no means rare along the Dutch coast. The writer collected the species on the seadike of Oude Schild (Island of Texel), near Den

Helder, on the Hondsbosse Zeewering near Petten and on the northern mole of Ymuiden. It was found near Den Helder mainly on woodwork, forming together with *Bangia atropurpurea* f. *fuscopurpurea* and *Urospora isogona* the vegetation of the splash-zone.

Contrary to both last mentioned species, it was also found, in the littoral belt, and even rather numerous on the stones near low water mark, in the *Polysiphonia-Chaetomorpha*-association. The species prefers localities exposed to the surf.

Though the majority of the specimens was collected in winter, the species was observed also in summer. The growth-period of the species depends to a high degree on the weather conditions.

The species is widely distributed in the northern Atlantic; it is also recorded from the North American coast of the Pacific.

Desmotrichum undulatum (J. Ag.) Reinke

In June 1952 this species was discovered by the author in the Island of Schiermonnikoog. Most of the collected plants were young. Only two fertil specimens were among them.

The steril plants are filiform and 5–12 mm long. The smallest specimens are 60–80 μ broad, the larger 300–500 μ .The alga consists of 10–15 cell-rows and is 2 cell-layers thick. It bears a good number of hairs.

The thallus is ribbon-shaped in the fertil specimens and consists of 2–4 cell-layers. The plants have a length of 75 and 18 mm and a breadth of 3–4 and 2 mm respectively. The largest plant bears abundant unilocular as well as plurilocular sporangia; among them a few scattered hairs can be observed. The other plant possesses unilocular sporangia in the basal part only.

The species was collected in a large creek through the Oosterkwelder at Schiermonnikoog. It was attached to rhizoms of *Zostera marina*, together with *Ectocarpus confervoides* f. *siliculosa*, *Petalonia fascia*, *Leathesia difformis*, *Polysiphonia urceolata* and a few other algae.

In the herbarium of the author another specimen is preserved, collected by him near Oosterend, Island of Terschelling, in July 1950.

Desmotrichum undulatum occurs in the northern part of the Atlantic as well as along the North-American Pacific coast.

Desmarestia viridis (Müll.) Lamour.

Mr Mulder sent to the author a fine specimen of an alga, which could be identified as *Desmarestia viridis*. It was collected in April 1952 on a pontoon at Wemeldinge, Island of Zuid-Beveland, slightly below the waterlevel.

This annual species attains its development in spring and early summer.

The species is common in the northern Atlantic, along the European coast as well as on the coast of North America.

Antithamnion plumula (Ellis) Thuret

The occurrence of this alga along the Dutch coast has been stated in July 1952 by the author. Before that time the species had been seen on drifting objects, washed ashore on the beach (LUCAS, 1950). In 1952 some specimens were collected on a pontoon in the port of Vlissingen, Island of Walcheren, ca 1 m below water level.

Antithamnion plumula is widely distributed in the northern Atlantic and in the Mediterranean. According to BØRGESEN and JONSSON (1908) it is probably a cosmopolite.

Ahnfeltia plicata (Huds.) Fries

This species had been collected twice on the seadike of Den Helder. The first find dates from May 1952 when several specimens were discovered near mean low watermark of springtide in the *Polysiphonia-Chaetomorpha*-association, already described by VAN GOOR (1923). This association which occurs between mean low water mark of neap tide and mean low water mark of spring tide is characterized by *Polysiphonia urceolata* f. *roseola*, a species which is often dominant, *Chaetomorpha aerea*, *Cladophora rupestris* and a considerable number of other algae. *Ahnfeltia* prefers the lowest place in this vegetation, where it is accompanied especially by *Chondrus crispus*, *Phyllophora membranifolia* and a number of Bryozoa and Hydrozoa. This vegetation resembles somewhat the "*Ahnfeltia-Phyllophora* formation" which was described by KYLIN (1907) from the West coast of Sweden.

Ahnfeltia was found growing exclusively on the upper-surface of flat stones, in dense, rigid, dark, purplish coloured tufts, originating from a violet-blue coloured crust. That crust was closely attached to the substrate. Stones covered by "*Polydora-mud*" were clearly avoided. The height of the tufts varies from 3–5 cm. According to ROSENVINGE (1931) *Ahnfeltia* is increasing in length in the Danish waters circa 3 cm in one year. Therefore we may suppose the Dutch specimens have surely an age of a year. Many plants were densely overgrown by specimens of the Bryozoan *Electra pilosa*, the Hydroid *Laomedea* spec., young specimens of *Mytilus edulis*, whereas the Amphipod *Jassa falcata* had built its tubes between the fronds.

The other find was a single specimen, densely overgrown with *Laomedea*, collected near Huisduinen in July 1952 in a similar vegetation at the same level.

All plants appeared to be sterile. The area of *Ahnfeltia* is very extended. The species is characterized by BØRGESEN and JONSSON (1908) as boreal-arctic, for it occurs along the European as well as the North-American Atlantic coast. Further, *Ahnfeltia* is recorded from the North-American Pacific coast (SETCHELL and GARDNER, 1903) and from Karachi (ANAND, 1943).

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NOTES ON SOME SOUTH AMERICAN SOLANACEAE

BY

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(Received Febr. 13th 1954)

Solanum Schlechtendialianum Walp., Rep. III (1844-45) p. 61; Dunal in A. DC. Prodr. XIII I (1852) p. 109—*Solanum geminifolium* (nec *geminiflorum* ut errore typogr.) Schlechtendal in Linnaea V (1830) p. 112, VIII p. 255 non Thonner;—*Solanum subsessile* Klotsch in Schomburgk Reisen Br. Guiana III (1848) p. 964 nomen nudum; —*Solanum clathratum* Sendtn. in Mart. Fl. Bras. X (1846) p. 35 ex Schulz;—*Solanum fragile* Wright apud Griseb., Cat. (1866) p. 189;—*Solanum salviaefolium* Lam. sensu Schulz in Urban, Symb. Ant. VI (1909) p. 177 et auctoribus sequentibus, non Lam.

Examined specimens:

French Guiana: Acarouany, Sagot 898 fl. April 1856 (P)
Br. Guiana: Schomburgk 1526, in ripa fluminis Barama fl. Oct. and Nov., (P) named *Solanum subsessile* Klotsch in Schomburgk, Reisen Br. Guiana III (1848) p. 964 nomen nudum, nr. cited by Schulz l.c.); Roraima, Schomburgk 859. (P) [1]).

Cuba: western part, Wright 3024; typus of *Solanum fragile* Wright apud Grisebach 1866 (S); San Blas, Jack 5924 fl. April; Las Animas Valley, Rangel, Leon 12585 fr. June, the two latter specimens from the Herbario del Colegio de la Salle, Havanna, Cuba.

Further distribution: Central America, Brazil.

In the Paris herbarium I had the opportunity to study the type of *Solanum salviaefolium* Lam. 1793, which proved to belong to *Solanum asperum* Rich. 1792 (syn. *Solanum radula* Vahl 1798). The species was quite correctly interpreted by Dunal in A.D.C. Prodr. XIII I (1852) p. 107. Poiret in Lamarcks Encycl. IV p. 280 describes the leaves as "retrécies" at the base, nevertheless, the interpretation of SCHULZ has been followed in recent Central American Floras, though, from the specimens enumerated by SCHULZ, it is clear that he did not personally examine the type of Lamarck.

Solanum velutinum Dunal apud Poir., Encycl. Suppl. III (1813) p. 766; Dunal in A.DC. Prodr. XIII I (1852) p. 231;—*Solanum*

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[1] In Kew I saw still several later collections from Br. Guiana: Jenman 4780, 7379; Cuyuni R. F. D. 1081; Mazaruni R., F.D. 4780.

brachybotryon Dunal (1952) t.c.p. 212;—*Solanum surinamense* Sendt. in Martius Fl. Bras. X (1846) p. 103 t. 7, fig. 54, non *S. surinamense* Steud. 1843;—*Solanum canocinereum* Dunal l.c. p. 213.

Fr. Guiana, Cayenne, Martin, type of *S. velutinum* Dunal (P); Acarouany, Sagot 457, 6; Crique Jacques: Wachenheim nr. 12 fl. Sept., all in P.

Suriname: Hostmann 1008, cited as type of *Solanum brachybotryon* Dunal, this or the following nr. probably also the type of *S. canocinereum* Dunal; Hostmann 1013 ex Dunal; Kappler ed. Hohenacker nr. 1008 (P).

There seems to be some confusion in the nrs. 1008 and 1013 of Hostmann, there are specimens of *Solanum subinerme* Jacq. bearing the same nr. Hostmann 1013. *Solanum canocinereum* Dunal is based on *Solanum surinamense* Sendtn. non Steud; the type is an unnumbered specimen of Hostmann apparently not seen by Dunal personally; the present author has written to the director of the Munchen herbarium whether the type specimen was possibly deposited in that herbarium, but the answer was in the negative.

By its softly pubescent twigs and leaves (the stellate hairs bear an elongated central radius) and by its 5-fid calyx the species is readily recognized from the allied *S. paludosum* Moric. a Brazilian species recently collected in all three Guianas. (in Fr. Guiana by Sagot).

Solanum pachyneuroides Amsh. n. sp.;—*Solanum pachyneurum* Schulz var. *glabrescens* Schulz in Urban, Symb. Nat. VI (1909) p. 196.

Ramuli apice sparse pubescentes pilis stellatis pauciradiatis sessilibus mox glabrescentes. Folia adulta elliptica vel oblonga, sinuato-lobata, 6–9 cm longa, 3–4 cm lata, subcoriacea, reticulata, glaberrima, sparse aculeata; nervis lateralibus utrinque 6–8, patentibus,supra ut subtus acute prominulis, arcuato-anastomosantibus, ramulo altero in marginem decurrente, bene conspicuo. Aculei parvi, sed longiores quam in *S. pachyneuro*, ramulorum basi incrassati, usque ad 3 mm longi, foliorum et petiolorum subteretes, graciles, usque ad 4(–5) mm longi. Bacca ex Schulz 20–25 mm in diameter. Inflorescentia et calyx glaber; petala margine tantum pubescentia.

Cuba: Prov. Oriente, Sierra de Cristal, ad Rio Labisa, in manacales (Ekman 6879 fl. March det. Schulz; Guantanamo, Monte Libanon, San Fernandez, in pinetis, 700 m alt., fl. Dec., Ekman nr. 10300 (flowers small, blueish-violaceous) det. Schulz. Road to Delta mine, Punta Gorda, Moa Region, Or., Bros. Alain, Clemente et Chrysogone fl. July 1949, nr. A. 912, typus! ibidem, Br. Victorin, Clemente et Alain 21703 ster (the two latter specimens from the Herbario del Colegio de la Salle, Havana).

In *S. pachyneurum* O.E. Schulz the leaves are stellate-puberulous on both sides with minute stellate hairs provided with a central disc. There are about 10(–13) subhorizontal pairs of arcuate-anastomosing lateral nerves; the branch that runs to the margin is inconspicuous. The berry is only 7 mm in diameter. However, the type of *Solanum pachyneurum* var. *glabrescens* Schulz, Wright 382 p.p., could not be examined, only the two nrs. of Ekman determinated by Schulz himself as such, and therefore Bro. Alain, Clemente et Chrysogone nr. A. 912 fl., is here taken as the type. Both species agree in their abbreviated lateral raceme-like inflorescences with small, not more than 1 cm long blueish flowers that are probably polygamous. The type of *S. pachyneuroides* bears only male flowers. The Latin diagnosis gives only the characters which distinguish this species from *S. pachyneurum* Schulz; from this latter species dolichostylous and brachystylous flowers are known, but the difference in the flowers is not shown in other characters. [1]) In Solanum pachyneurum the calyx and the petals are densely stellate-pubescent outside.

Melananthus cubensis Urban in Fedde, Rep. XVIII (1922) p. 23. Cuba: Prov. Oriente, near Holguin, Ekman 3297, typus (S), 7587 (S); Bro. Leon 15698 and 16927 fl. July; Prov. Camaguey, Santagana, 5 KM east of Camaguey city, Ekman 15330, and a few other nrs of Ekman collected near the first named locality.
Brazil: Rio Branco, Ule 7854 (L).

The discovery of this species by Ule in 1909 in Northern Brazil seems to be worth mentioning, since this species was hitherto only known from Cuba. The second and only other species known from Brazil is the Southern Brazilian *M. fasciculata* (Benth.) Sol. A key to these two species may be given here:

a Leaves narrowly spathulate, up to 2 cm long. Corolla 5 mm long; fertile stamens 4, didynamous; fruit bivalved, nearly smooth. *M. fasciculata*

b Leaves linear, not more than 1 cm long. Corolla 2–3 mm long; fertile stamens 2; fruit indehiscent, conspicuously tuberculate. *M. cubensis*

Both species are slender herbs much resembling a species of *Schwenckia*, and in the first place differing from that genus by the 1-seeded fruit, and 1-ovulate ovarium. A third species, *M. guatemalensis* Bentham ex Hemsley, from Guatemala and apparently very rare, has according to the description linear leaves, 4 fertile stamens, and a conspicuously tuberculate fruit. (During the revision of this alinea my attention was drawn to the description of a fourth species, *M. luetzelburgii* Süsseng., also from Brasil. This species is according to the description very nearly allied to M. cubensis Urb. The only differences seem to be the more deeply divided nearly 5-fid calyx and the distinctly unequal corolla lobes.)

Litterature: Solereder in Berichte Deutsche Bot. Geselsch. IX (1891) p. 65–85.

The genus **Lycianthes** (Dunal) Hassl. When in 1920 Bitter published his monograph of "Die Gattung Lycianthes" in Abh. Naturw. Ver.

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[1] I am alluding here to the fact that the calyx in the fertile flowers is not more prickly and not more accrescent than in the sterile flowers.

Bremen 24 (1920) p. 292–250, he was still in doubt about the identity of the genus *Parascopolia* Baill. This genus was published by Baillon in Baillon, Hist. des Plantes IX (1888) p. 338 with as only species *Parascopolia acapulcensis* Baillon from Mexico. Afterwards Bitter visited the Paris herbarium, where the type is deposited, and he saw that *Parascopolia acapulcensis* Baillon shows all the characters of the genus *Lycianthes*, but he apparently died before he could publish any of the new combinations already made by him under the genus name of *Parascopolia* Baill. in the Paris herbarium. The name Lycianthes (Dunal) Hassl. has been used by most authors of regional floras, in America as well as in Asia; the type species is Lycianthes lycioides (L.) Hassl. in Ann. Conserv. et Jardin Bot. Geneve XX (1917) p. 180. Morton, who in Field Museum of Nat. History, Bot. Vol. XVIII (1938) p. 1056 accepted the genus Lycianthes, came, after a more prolonged study in Contr. U.S. Nat. Herb. 29.1 (1944) to the conclusion that the segregation of this genus from Solanum L. is not justified. For the moment I hesitate to express a personal opinion, but in any case the name *Parascopolia* Baill. can best be added to the nomina rejicienda.

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L'ANALYSE DES CARRÉS PERMANENTS

PAR

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(Wageningen)

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Pour étudier le développement de la végétation en un lieu donné, au cours des saisons et d'année en année, il est nécessaire de délimiter le "carré permanent" au moyen de repères bien visibles, et de décrire avec précision le tapis végétal à des périodes déterminées.

La fixation des aspects successifs de la végétation peut s'effectuer, d'une part en repèrant sur un graphique la position de toutes les plantes, d'autre part en prenant une série de photographies sous le même angle. Ces deux méthodes sont entachées d'inconvénients d'ordre pratique, et ne sont que rarement appliquées. En général, on se contente d'effectuer des "relevés" classiques, selon la méthode de Braun-Blanquet. Cette dernière méthode a donné pleine satisfaction pour les études courantes de phyto-sociologie: pour faciliter la comparaison des résultats, il est souhaitable qu'elle soit appliquée par le plus grand nombre possible de chercheurs.

Cependant l'étude des carrés permanents a montré qu'il était désirable d'atteindre une plus grande précision. On a souvent l'impression que les fluctuations de l'abondance relative des espèces ne ressortent pas suffisamment dans le tableau. Aussi, prenant comme base l'échelle de Braun-Blanquet, plusieurs phytosociologues de Wageningen ont-ils mis au point une méthode plus précise. Il va de soi que cette dernière est plus laborieuse que la méthode classique, et en conséquence ne se justifie que pour des cas spéciaux.

Tout d'abord, nous avons modifié l'échelle combinée de l'abondance-dominance à 6 degrés de Braun-Blanquet, et adopté une "échelle décimale", qui est appliquée séparément à l'estimation de l'abondance et de la dominance, soit l'une d'elles, soit l'une après l'autre*. Nous obtenons ainsi les symboles suivants:

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* Cette possibilité est élaborée plus en détail par R. Nègre („Intéret de noter séparément l'abondance et la dominance en Phytosociologie"; Recueil des Traveaux des Laboratoires de Botanique, Géologie et Zoologie de la Faculté des Sciences de l'Université de Montpellier, Série Botanique, Fasc. 5, 1952) .Cette publication, contenant bien d'autres remarques importantes, ne tira notre attention qu'après cet lignes-ci furent écrites. La proposition de Nègre d'introduire une notation séparée pour le recouvrement radiculaire, n'est pas applicable dans le cas des carrés permanents, de même que dans un nombre d'autres cas.

Echelle decimale				Echelle de Braun–Blanquet	
r	(raro) recouvrement	< 5 %	—	individus sporadiques	+
p	(paululum) ,,	< 5 %	—	,, peu nombreux	+
a	(amplius) ,,	< 5 %	—	,, assez nombreux	1
m	(multum) ,,	< 5 %	—	,, nombreux	2
01	recouvrement	5–15 %	—	nombre d'individus quelconque	2
02	,,	15–25 %	—	,, ,, ,,	2
03	,,	25–35 %	—	,, ,, ,,	3
04	,,	35–45 %	—	,, ,, ,,	3
05	,,	45–55 %	—	,, ,, ,,	3–4
06	,,	55–65 %	—	,, ,, ,,	4
08	,,	65–75 %	—	,, ,, ,,	4
07	,,	75–85 %	—	,, ,, ,,	5
09	,,	85–95 %	—	,, ,, ,,	5
10	,,	95–100 %	—	,, ,, ,,	5

Les limites des tensions de recouvrement ont été choisies de façon à permettre l'estime en dixièmes de la superficie totale, et à pouvoir noter instantanément le chiffre obtenu. Les espèces atteignantes une tension de recouvrement de 5 % au moins ("Vegetationsformende Arten") reçoivent ainsi un *chiffre*, les autres se distinguent immédiatement par une *lettre*. D'autre part on note pour les espèces méritant le même chiffre ou la même lettre, l'ordre d'importance de leur abondance ou dominance respective, ce qui en pratique est facile à constater, et les espèces sont classées dans cet ordre dans le tableau. Evidemment, le numéro d'ordre d'une espèce dans un relevé donné, n'a qu'une valeur relative, cependant cette relativité peut être éliminée en grande partie en ramenant le nombre total des espèces des relevés différents à un chiffre constant, p.e. 60 ou 100: ainsi, même lorsque le nombre des espèces varie, ou lorsque les relevés sont très riches, peut-on obtenir une échelle très sensible des modifications survenues. Il est à peine besoin de souligner que chaque strate (strate arborescente, arbustive, herbacée etc.) doit être estimée séparément, et que, en réunissant plusieurs relevés en un tableau, le classement exact des espèces ne peut être effectué que par rapport à un seul relevé. Pour les autres relevés, le numéro d'ordre des espèces (éventuellement le numéro d'ordre ramené à 60 ou 100 espèces) peut être indiqué dans leurs colonnes respectives. Cette méthode est donc également utilisable pour la comparaison de différents types de végétation avec un ou plusieurs "relevés standards", par exemple pour l'étude minutieuse d'une série de transitions graduelles entre deux types aux fins de recherches écologiques. L'établissement des numéros d'ordre est encore possible lorsque l'échelle décimale n'est plus d'application.

Attirons particulièrement l'attention sur le fait que certaines espèces ligneuses, des lianes et beaucoup d'espèces herbacées peuvent être représentées dans différentes strates, aussi bien aériennes que souterraines. Dans ces strates les conditions écologiques varient fortement (lumière, humidité, concurrence radiculaire, concurrence par rapport aux animaux pollinisateurs et transporteurs de graines, etc.). Aussi les individus d'une même espèce distribuées dans différentes strates, réagissent-ils à plus d'un égard, comme des espèces différentes. Il peut se faire que la présence d'une espèce dans une strate déterminée soit caractéristique pour un type de végétation donné, tandis que sa présence dans d'autres strates n'ait rien de particulier. En cas de succession, non seulement la composition floristique et les rapports de masse subissent-ils des modifications, mais également la stratification est modifiée. Des phénomènes semblables s'observent pour les aspects saisonniers et dans les zonations. En conséquence, il est souhaitable en de nombreux cas, de différencier les diverses strates d'une manière plus précise, en indiquant autant que possible la hauteur des strates ou des différentes espèces. Dans un tableau, on peut ventiler une même espèce dans différents groupes, selon la strate où elle végète. Pour le calcul de la "valeur de groupe" d'un nombre d'espèces de grande affinité sociologique selon les méthodes de Schwickerath ou de Tüxen et Ellenberg, il convient de compter autant de fois une espèce qu'il y a de strates où elle apparait. Ainsi la différenciation structurelle se présente plus nettement.

L'estimation de la sociabilité selon l'échelle de Braun-Blanquet ne requiert pas d'être élaborée plus en détail. Cependant la sociabilité ne donne pas une idée suffisamment précise de la dispersion des espèces au sein du carré d'essai. En effet aucun type de végétation n'est parfaitement homogène. En se montrant trop exigeant à cet égard, on n'obtiendra que des relevés extrêmement pauvres avec les désavantages que cela comporte, à supposer toutefois que l'on ait le libre choix du carré d'essai, ce qui est loin d'être la règle. Il convient cependant de décrire autant que faire se peut, le degré d'hétérogénité du "carré", même si on ne désire pas utiliser la méthode extrêmement laborieuse des graphiques. Cela serait aussi profitable pour l'interprétation de nos relevés par des chercheurs travaillant selon la méthode de la dominance, et de plus cette procédure permettrait l'utilisation de relevés qui s'avéreraient ultérieurement être un mélange de deux types de végétation différent.

Le problème est résolu d'une manière assez simple de la manière suivante.

Supposons qu'un relevé comporte les espèces *a* à *k*. Les espèces *a*, *c*, *d*, et *h* diffèrent fortement entr'elles quant à la dominance, cependant toutes sont régulièrement dispersées dans le carré. L'espèce *b* n'est representée que dans une zone déterminée du carré; les espèces *e*, *i*, *j* et *k* sont dispersées le long des bords du carré; les espèces *f* et *g* se trouvent réunies dans des autres endroits. Cette dispersion est signalée par le symbole loc (local), suivi d'une chiffre se rapportant au groupe considéré des espèces irrégulierement dispersées.

Le relevé de l'exemple précité, se présente alors ainsi:

a	
b	loc 1
c	
d	
e	loc 2
f	loc 3
g	loc 3
h	
i	loc 2
j	loc 2
k	loc 2

Extrait d'un relevé, fait dans un forêt de Pseudotsuga taxifolia à "Schovenhorst" (Putten, prov. de Gueldre). Strate herbacée et muscinale: 50 %.

No. = Numéro d'ordre dans chaque groupe d'espèces de chiffres ou lettres identiques, tel que noté dans le terrain.

Forme provisoire

No.			
	Oxalis acetosella		04.3
	Rubus spec.	loc 2	01.2
1	Hedera helix	loc 1	p.2
1	Dryopteris austriaca		r.2
4	Epilobium angustifolium	loc 2	p.2
3	Carex pilulifera	loc 2	p.2
6	Lonicera periclymenum		p.2
7	Pseudotsuga taxifolia		p.1
2	Vaccinium myrtillus	loc 5	r.2
5	Calluna vulgaris	loc 2	p.2
	Pleurozium schreberi	loc 3	01.3
	Hypnum cupressiforme	loc 4	a.2
8	Dicranella heteromalla	loc 4	p.2
2	Deschampsia flexuosa	loc 5	p.2

Forme définitive (dans le tableau)

Oxalis acetosella		04.3
Rubus spec.	loc 2	01.2
Pleurozium schreberi	loc 3	01.3
Hypnum cupressiforme	loc 4	a.2
Hedera helix	loc 1	p.2
Deschampsia flexuosa	loc 5	p.2
Carex pilulifera	loc 2	p.2
Epilobium angustifolium	loc 2	p.2
Calluna vulgaris	loc 2	p.2
Lonicera periclymenum		p.2
Pseudotsuga taxifolia		p.1
Dicranella heteromalla	loc 4	p.2
Dryopteris austriaca		r.2
Vaccinium myrtillus	loc 5	r.2

Forme selon la méthode de Braun–Blanquet

Oxalis acetosella	3.3
Rubus spec.	2.2
Pleurozium schreberi	2.3
Hypnum cupressiforme	1.2
Hedera helix	x.2
Dryopteris austriaca	x.2
Epilobium angustifolium	x.2
Carex pilulifera	x.2
Lonicera periclymenum	x.2
Pseudotsuga taxifolia	x.1
Vaccinium myrtillus	x.2
Calluna vulgaris	x.2
Dicranella heteromalla	x.2
Deschampsia flexuosa	x.2

Notre méthode parait à première vue assez compliquée, à la pratique cependant elle s'est avérée satisfaisante, et n'impose aucun effort extraordinaire à la mémoire de l'observateur. L'on effectuera de préférence des essais dans des types de végétation peu compliqués.

Les relevés peuvent être ramenés au type classique, si besoin en est.

Finalement je remercie M. W. Mullenders pour sa traduction consciencieuse de ces lignes.

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MISCELLANEOUS NOTES ON SCIRPUS LACUSTRIS L. SENSU LAT. IN THE NETHERLANDS

BY

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With Plates 24—26

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This paper chiefly deals with the problem whether or not *Scirpus lacustris* L. and *S. tabernaemontani* Gmel. should be considered as separate species. As to this question, quite different opinions have been developed in literature. On the strength of an examination of the specimens occurring in the Netherlands, in this paper they are regarded as ecotypes (subspecies) of the ecospecies *S. lacustris* L. *sensu lat.*, which will be explained below. In addition data are given on the polymorphy, the distribution and the hybrids with *S. triqueter* L. in the Netherlands.

The examinations were made on living plants and herbarium specimens. During my endeavours I had the opportunity of consulting the collection preserved in the Rijksherbarium at Leyden, in which among others are inserted the herbaria Jansen and Wachter, Kern and Reichgelt, Kloos, Van Ooststroom, Van Soest, Vervoort and De Bruyn. Moreover, I was able to study the herbaria of the Royal Botanical Society of the Netherlands at Leyden, the Botanical Museum and Herbarium at Utrecht, the Hugo de Vries Laboratory at Amsterdam, the Botanical Laboratory at Groningen, the Plant Taxonomical and Geobotanical Institute at Wageningen, the Museum of Natural History at Maastricht and the Department of Botany of the Northeasternpolderworks at Kampen.

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Different opinions on the systematical status of *S. lacustris* L. *sensu lat.*

In 1753 Linnaeus described *S. lacustris*, that is in this paper the ssp. *lacustris*. Gmelin (1805) made the description of *S. tabernaemontani* (syn. *S. glaucus* Smith, 1812). C. Hartman (1848) classified *S. tabernaemontani* for the first time as a subspecies of *S. lacustris*, which he called ssp. *glaucus* (Smith) Hartman. However, Roth already described in 1788 the var. *β .minor* of *S. lacustris* L., which is obviously identical with the ssp. *glaucus* (Roth, 1802; Neilreich, 1859).

In the nineteenth century, especially Mertens and Koch (1823), Custor (1830), Kunth (1837) and Koch (1837, 1844) considered these subspecies as separate species. On the other hand, Fries (1828), Döll (1843), Andersson (1849), C. J. Hartman (1849), Meyer (1849), Parlatore (1852), Grenier and Godron (1855–'56), Neilreich (1859), Böckeler (1870) etc. united these entities into one species in view of the strong resemblance, the unstable characteristics, the merging into one another under the influence of the environment or the occurrence of intermediate forms.

Fries, Andersson, C. J. Hartman and Böckeler considered the ssp. *glaucus* as the var. *β. glaucus* of *S. lacustris*.

Döll divided *S. lacustris sensu lat.* (as *S. lacustris* Döll) into the following four varieties:

a. *vulgaris*, identical with *S. lacustris* L.
b. *minor*, smaller than a, stems bluntly triangular above, glumes somewhat asperous and in some spikelets scattered flowers with 2 stigmas.
c. *trigonus*, stems bluntly triangular above, at the tip bearded connectiva and mostly 2 stigmas, further as b.
d. *tabernaemontani*, with glaucous and at the apex faintly triangular stems, connectiva at the tip practically not bearded and 2 stigmas.

In the wet year of 1838 Döll made the observation that from the var. d. *tabernaemontani* the stems had turned greener, higher and rounder, whilst in every spikelet flowers with two and three stigmas occurred. It follows that under the influence of changing environmental conditions some characteristics of *tabernaemontani* had altered into those of *lacustris*. This is in agreement with the opinion of Neilreich (1859), who considered the var. *α. major* Roth (ssp. *lacustris*) as the aquatic form and the var. *β. minor* Roth (ssp. *glaucus*) as the terrestrial. Neilreich remarked: "Zwei vom Wasserstande bedingte und daher vielfach in einander übergehende Varietäten". From some statements of Meyer (1849) it seems likely that he considered the var. c. *tabernaemontani* (ssp. *glaucus*) to be a modification owing to a saline habitat. Probably also Grenier and Godron (1855–'56) had thought of these subspecies as modifications. They distinguished the following varieties:

α. *genuinus* Gren. et Godr. (ssp. *lacustris*), with 3 stigmas, trigonous fruits; dark-green robust plant, growing in water.

β. *digynus* Godr. (ssp. *glaucus*), with 2 stigmas, fruits compressed and smaller than in α; more slender than α, glaucous, growing on in winter flooded areas and in the mountains. Their following remark regarding *S. tabernaemontani* is worth quoting: "Aucun des caractères par lesquels on a voulu le distinguer du *S. lacustris* n'est constant".

PARLATORE (1852) pointed out that these plants are forms of one species which do not even have the status of varieties in view of the unstable characteristics, e.g. the number of stigmas, the asperity of the glumes and the length of the bearded points of the connectiva.

However, ASCHERSON and GRAEBNER (1902–'04) made a statement regarding the uniting into the same species as a consequence of the intermediates and the unstable characteristics: "Wir haben uns jedoch bisher davon nicht überzeugen können". They maintained the species *S. lacustris* L. and *S. tabernaemontani* Gmel., which had been accepted by most of the later botanists.

According to LOUSLEY (1931) the hybrid of *S. lacustris* L. and *S. tabernaemontani* Gmel. has been known in Germany and Denmark for a considerable number of years in localities where it grows with the parents. However, the authors BUCHENAU (1877), FOCKE (1881) and BRÜGGER (1882), cited by LOUSLEY, have recorded this hybrid only from Bremen in Germany. Undoubtedly FOCKE and BRÜGGER quoted BUCHENAU. BUCHENAU described the hybrid as follows: „hochwüchsig, grasgrün: Deckspelzen rotbraun, nicht rauh punktiert; Narben 3. Fr. sehr spärlich entwickelt, zwischen denen beider Arten die Mitte haltend; an der Innenseite des Hollerdeiches bei Kattrepel".

Although the affinity of the parents is close and they occur together in several localities, it is noteworthy that the hybrid was found only in one place. On the other hand the hybrid between the ssp. *lacustris* and *S. triqueter* L., which differ from each other considerably in morphological characteristics, is recorded from several localities. This may be the result of the fact that the hybrid mentioned first is not easily recognizable.

The scarce fruit formation is the only characteristic in the description of BUCHENAU that should be regarded as an argument in favour of the hybrid nature. But as nothing is known on the germinative power of the seeds and the viability of the plants developing from these seeds, the scarce fruit formation is no proof for the hybrid origin. The more so as the present writer now and then observed a scarce fruit formation in the ssp. *lacustris* and *glaucus*, although in other respects these plants did not differ from fertile ones.

Besides the hybrid, intermediates were recorded from several localities (DÖLL, 1843; MEYER, 1849; NEILREICH, 1859). In this connection the following statement was made by FOCKE (1881): "*S. lacustris* L. × *S. Tabernaemontani* Gm. ist ein wenig fruchtbare Mittelform, bei Bremen beobachtet. An andern Orten hat man Uebergänge gesehen, die nicht als Bastarde gedeutet werden".

From this review of the literature, it becomes quite clear that the opinions with regard to the systematical status of the ssp. *lacustris* and *glaucus* are quite different. However, it is open to question whether or not the specimens studied by Döll, Neilreich and others might be compared with the Dutch material. As appears from the literature, the characteristics of the ssp. *glaucus* are much more unstable in Central Europe than in the Netherlands. Moreover, in our country this subspecies reaches its optimal development in a brackish habitat with a range of 0.1–10$^0/_{00}$ chlorine or in an environment that was recently brackish, e.g. the coast of the Yssellake. On the contrary, in Central Europe the ssp. *glaucus* seems to grow in a fresh habitat under drier conditions than the ssp. *lacustris*. It is not known, however, if this contrast between the Dutch and Central European specimens is the result of environmental or genotypical differences. In no case, however, in the Netherlands these subspecies are modifications. In spite of the plasticity of *S. lacustris* L. *sensu lat.* (Glück, 1923; Seidel, 1952*a*) it must in this connection not be overlooked that the modifiable varieties, described by Döll, Neilreich, Grenier and Godron and others, might be in fact cross-breeds of the ssp. *lacustris* and *glaucus* or hybrids between *S. lacustris* L. *sensu lat.* and *S. triqueter* L. (Lousley, 1931).

It follows that it is desirable to discuss the arguments which must be advanced in order to prove whether the two subspecies belong to the same or two different species.

In the opinion of Danser (1950) the essence of the large species is an intermixing community or commiscuum. By this he understands a collection of forms which are mutually connected by the capacity of intermixing. Intermixing is the phenomenon that two forms which are crossed yield in the first generation more or less intermediate forms, which on selfing or fertilization by sister specimens, and also on back-crossing with one of the stem-forms, assume a great polymorphy, so that after a few generations the boundaries between the originally crossed forms are obliterated. In the same commiscuum all coinciding forms, both in wild growth and cultivated, are connected by series of intermediate forms. In addition, forms belonging to one commiscuum will, as a rule, yield fertile cross-breeds, whereas forms belonging to different commiscua will not. Thus the criteria of the systematists for distinguishing species coincide in the concept commiscuum.

However, it is rather extreme to look upon the absence of gradation, or the failure to breed together and to produce fertile offspring, as the only criteria of specific distinction. On that ground, besides the commiscuum-concept, also the morphological resemblance, the number of chromosomes and the distribution will be considered in discussing the species-concept of *S. lacustris* L. *sensu lat.*

In this connection, it is important that from the coast of the Yssellake in the Netherlands, an intermediate form with undiminished fertility and the same chromosome number as the ssp. *lacustris* and *glaucus* has been recorded of late years (tables 1, 2 and 3). Moreover, the characteristics of this intermediate proved to be of a stable nature. Seeing that the plants grown from the seeds of this intermediate are morphologically identical with the plants of the preceding generations, the intermediate should not be regarded as the F 1 from the crossing of the subspecies. Furthermore, the possibility exists that artificially cross-breeds of the subspecies are achieved (Miss Dr K. Seidel, in a letter, 13 October 1953). Evidences for such cross-breeding in wild growth is provided by the observation that in the Netherlands highly fertile plants with overlapping characteristics are mainly found in areas where the subspecies grow together. It follows that in all probability the intermediate, which has obliterated the boundaries between the two subspecies, may be regarded as the result of "introgressive hybridization" *sensu* Anderson and Hubricht (1938) (Heiser, 1949), which means the gradual infiltration of the germplasm of one subspecies into that of the other through the repeated back-crossing of the cross-breed to one or both parents. According to the principle of Danser, it is evident now that the ssp. *lacustris* and *glaucus* belong to the same commiscuum. Furthermore, in table 1 the great morphological resemblance is shown, whilst also a gradation occurs as has been pointed out above. Moreover, it is a matter of fact that these subspecies reach their optimal development in different habitats, which means they are ecotypes *sensu* Turesson (1922). It follows that the ssp. *lacustris* and *glaucus* may be united into the same ecospecies, viz. *S. lacustris* L. *sensu lat.* An ample discussion of these data will be given below.

In spite of intermixing they usually remain distinct entities; in all probability owing to the fact that the chances of cross-breeds and back-crossings holding their own in competition with the parents are poor (Heiser, 1949). But as a consequence of the stable characteristics and the fertility, the intermediate from the coast of the Ysselake will be described in this paper as the ssp. *flevensis* of *S. lacustris* L. *sensu lat.*, which only by the intervention of man continues existence in the habitat of the ssp. *lacustris*.

It must also be pointed out that in the Netherlands the hybrids between *S. lacustris* L. *sensu lat.* and *S. triqueter* L. are recorded from several localities. Although, this hybrid swarm shows a considerable lack of uniformity in morphological characteristics as well as in fertility, they usually are of low fertility; this means *S. lacustris* L. *sensu lat.* and *S. triqueter* L. belong to separate commiscua. The morphological characteristics, too, are entirely different, whilst they partly reach their optimal development in the same habitat, viz. in the *Scirpetum maritimi* Tüxen of the faintly brackish to fresh tidal estuaries in the S.W. of the Netherlands. Hence they are regarded as separate species.

Some data on *S. lacustris* L. *sensu lat.* in the Netherlands

In the Netherlands the following three subspecies are distinguished:

1. **Scirpus lacustris** L. ssp. **lacustris**; Linnaeus, Sp. Pl., 48–49, 1753.

Although it appears that some characteristics of the ssp. *lacustris* may overlap with the other, these plants usually are determined

TABLE 1

Comparative summary of the characteristics of the three subspecies of *S. lacustris* L. *sensu lat.*

ssp. *lacustris*	ssp. *flevensis*	ssp. *glaucus*
Rhizomes hard and brittle; young white, later red-brown or dark red-brown; cells small (Plate 24)	Rhizomes fairly hard and tough; young white, later yellow- or red-brown; cells intermediate (Plate 24)	Rhizomes weak and tough; young white, later yellow or yellow-brown; cells large (Plate 24)
Stems round, $\frac{3}{4}$–$3\frac{1}{2}$ m high; light-, yellow- or dark-green or glaucous; not club-shaped below; diameter $\frac{3}{4}$–4 cm below	Stems round, $\frac{3}{4}$–$1\frac{1}{2}$ m high; glaucous; not club-shaped below; diameter $\frac{3}{4}$–$1\frac{1}{2}$ cm below	Stems round, sometimes faintly angular above, $\frac{1}{2}$–$2\frac{3}{4}$ m high; glaucous; robust plants club-shaped below; diameter $\frac{1}{2}$–6 cm below
If stems are cut off during or shortly after flowering they dry up yellow-green	As in the ssp. *lacustris*	If stems are cut off during or shortly after flowering they dry up yellow
Before and during flowering mostly 2–12 leaves with distinct leaf-blades (Plate 25); in the end the leaf-sheaths frayed	Before and during flowering 1–2 leaves with distinct leaf-blades (Plate 25); in the end the leaf-sheaths frayed	Before and during flowering only 1 leaf with a leaf-blade or leaf-blades wanting (Plate 25); the leaf-sheaths slightly frayed or not at all
Spikelets elongated or elongated-ovoid	As in the ssp. *lacustris*	Spikelets ovoid, elongated-ovoid or elongated
Glumes glabrous or only on the midrib asperous, usually brown	Glumes asperous on the midrib, especially the outer glumes also asperous near the midrib, brown	Usually all the outer glumes asperous, red-brown
Number of stigmas 3	Number of stigmas 2 and 3, resp. about 60 and 40 % in every spikelet; flowers with 3 stigmas especially at the tip of the spikelet	Usually number of stigmas 2, but rather much some flowers with 3
Connectiva bearded at the tip	Connectiva bearded at the tip, but usually shorter than in the ssp. *lacustris*	Connectiva usually very shortly bearded at the tip
Fruits bluntly trigonous, $2\frac{1}{2}$–3 mm long	Fruits faintly trigonous or compressed, about $2\frac{1}{2}$ mm long	Fruits compressed, about $2\frac{1}{2}$ mm long
Chromosome number 2 n = 42 (in Europe)	Chromosome number 2 n = 42	Chromosome number 2 n = 42

without much difficulty (table 1). It is a matter of fact that Netherlands specimens of the ssp. *lacustris* with aberrant characteristics have been rarely found, e.g. near Sleeuwijk along the Merwede, flowers mainly with 3 stigmas, glumes somewhat asperous, stems glaucous, leaf-sheaths frayed and distinct leaf-blades (herb. Kern and Reichgelt). But there is a difference in opinion with regard to the classification of the specimens from the Haringvliet and Hollands Diep in the S.W. of the Netherlands, as SEIDEL (1952*b*) placed the rushes from these brackish areas under *S. lacustris* L. (= ssp. *lacustris*). About this she states on page 304: "Die Variabilität ist aber grosz" and eight lines further on: "Es steht fest, dasz ihre Formen und Bastarde die Salinität, den Tidenhub und die Strömung prächtig vertragen". But SEIDEL does not point out what should be understood by the forms and hybrids of *S. lacustris* L. Any Dutch florist, however, would place the specimens from the Haringvliet and a part of the plants from the Hollands Diep under the ssp. *glaucus*. Upon inquiry Miss Dr K. Seidel declared that she is fully aware of the plasticity of *S. lacustris* L. *sensu lat.* This plasticity means that this taxon is easily affected by environmental conditions, e.g. in a dry habitat the leaf-blades of the ssp. *lacustris* are very short or completely wanting, the length of the stem is dependent upon the depth of the water (GLÜCK, 1923; SEIDEL, 1952*a*). Beside it, undoubtedly, fertile cross-breeds of the ssp. *lacustris* and *glaucus*, which are anemophiles, occur where they grow together, by which the overlapping characteristics in these subspecies may be explained, e.g. in the specimens of Kern and Reichgelt above-mentioned.

In spite of this, it is not clear to me on what grounds SEIDEL arranged these plants under *S. lacustris* L., as they have at the most the typical characteristics of the ssp. *glaucus*, which does not exclude sometimes the presence of any influence of the ssp. *lacustris* (table 1).

The plants discussed above have yellow, tough and weak rhizomes, with large cells (Plate 24). In the summer no new adventitious roots are developed, as has been described by SEIDEL (1952*a*) for the ssp. *glaucus*. The leaf-blades are short or wanting; the leaf-sheaths are somewhat frayed or not at all. The colour of the usually round stems is glaucous; at the base the stems are mostly club-shaped. If the stems are cut off during or shortly after flowering they dry up with a yellow colour; they die off late in autumn. During flowering nearly all the glumes are asperous. The number of stigmas is 2, but spikelets with scattered flowers with 3 stigmas are rather much found. At the tip the connectiva are short or very short-bearded. The fruits are compressed. According to table 1 these are characteristics of the ssp. *glaucus*.

The ssp. *lacustris* is a characteristic subspecies of the *Phragmition eurosibiricum* Tüxen, *em.* Braun-Blanquet et Sissingh. In the *Scirpeto-Phragmitetum medio-europaeum* Tüxen, which especially dominates in the "haf- en fluviatiel-district" *sensu* VAN SOEST (1923, 1924), and the *Scirpetum maritimi* Tüxen, from the nearly fresh to somewhat brackish tidal estuaries and the coast of the Yssellake between the

Ketel and the Zwarte Water, the ssp. *lacustris* reaches its optimal development. The *Scirpeto-Phragmitetum* is a soil-building association of fresh and stagnant water, rich in nutritive substances, till a depth of 1 m. The habitat of the ssp. *lacustris* in the tidal estuaries may be saline during high floods, which mostly happens in winter when the overground parts of the bulrushes have died, owing to which it is only of slight influence.

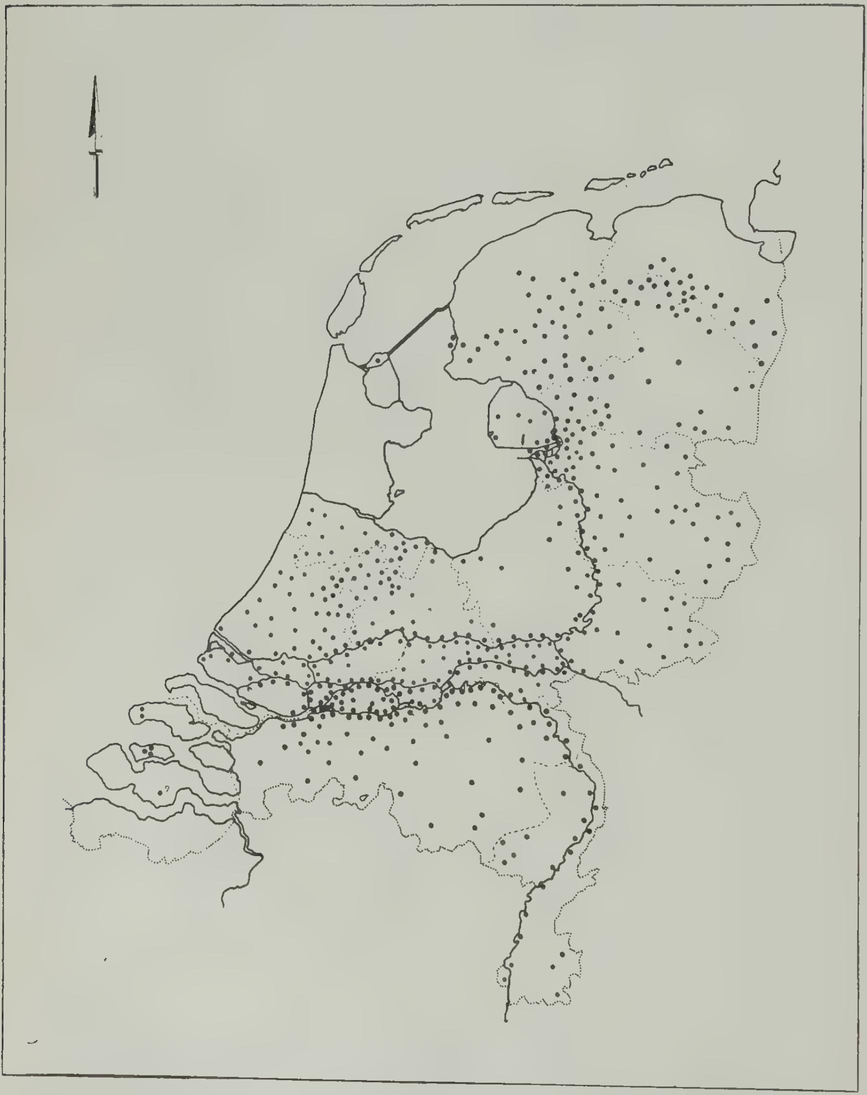

Fig. 1. Distribution of *Scirpus lacustris* L. ssp. *lacustris* in the Netherlands. The data on this map are due to the herbaria mentioned in this paper, the "Nederlandsch Kruidkundig Archief" and the observations of the writer

As appears from the distribution map (Fig. 1) the ssp. *lacustris* is wanting in the North of the provinces of Noord-Holland, with the exception of Wieringen, Friesland and Groningen, in the Wadden Islands, in Goeree and Flakkee and in several islands of the province of Zeeland; doubtlessly this is the result of the brackish environment in these areas. But it is possible that this subspecies will be recorded from some localities in the areas mentioned above. On the contrary this plant grows frequently along rivers, in peat-lakes, in the Kamperisland and in the lakes of the province of Friesland (Fig. 1). Especially in the Kamperisland and in the fresh tidal estuaries, bulrushes have been planted out for more than a century. On account of its domination in a fresh environment, the ssp. *lacustris* is considered in this paper as the ecotype of a fresh habitat. In a brackish environment several stages of the life-cycle are hampered, e.g. the growth of seedlings and flowering.

With regard to the factor "water" the ssp. *lacustris* is an amphiphyte *sensu* IVERSEN (1936), characterized by being able to thrive and flower both submersed and terrestrially, without reduction of vegetative parts.

In the Netherlands the following varieties and forms are distinguished:

var. **capitatus** Hausskn., Mitt. Geogr. Ges. Thür., 31, 6, 1888.

The inflorescences are capitate crowded (Plate 26 A). It is open to question, however, if this variety has any systematical value, as on the same rhizomes I observed stems with normal as well as with capitate inflorescences. Was found in the Netherlands in some localities, e.g. in the Kamperisland.

var. **foliosus** Rouy, Fl. Fr., 13, 374, 1912.

The leaf-blades are erect, rigid and composed of spongy tissue similar to that of the flowering-stems. Probably, this variety may be considered as a modification, engendered by external circumstances.

In the herbarium of the Plant Taxonomical and Geobotanical Institute, Wageningen, a specimen is preserved, that might be placed under this name. This plant was collected in July 1919, in a brooklet near De Steeg (leg. E. de Vries).

var. **glaucopsis** Bakker, nov. var.

Caules glauci.

(Type: Herb. Bot. Dep. N.E. polder nr. 1709; 1954, mouth of the Zwarte Water).

This variety has the same stem-colour, which is in all probability genotypically fixed, as the ssp. *glaucus*. Found along the mouth of the Zwarte Water, where glaucous clones grow mixed with green ones, and in a pool along the Overijsselse Vecht near Dalfsen. Seeing that also the stem-colour of the ssp. *lacustris* may vary in face of changing environmental conditions, no other colour-varieties are distinguished.

var. **pendulus** Bakker, nov. var.

Caules tenues et graciles, ad basin diametro 1–2 cm, sub inflorescentiis 2–3 mm. Inflorescentiae plerumque magnae, post anthesin nutantes. Hic varietas per multas formas intermedias in plantas erectas transgrediens.

(Type: Herb. Bot. Dep. N.E. polder nr. 1147; 1953, coastal area Kamperisland). See Plate 26 A.

This variety has been planted out in the coastal area of the Kamperisland (Yssellake), besides there are records of these plants from the Beulakker- and Belterwijde, Paterswolde, Vollenhove and the lake near Zuidlaren.

fo. **fluitans** (Coss. et Germ.) Glück, Beih. Bot. Clb., 39, 313–314, 1923.

Sheaths prolonged in leaf-blades ("Bandblätter" *sensu* GLÜCK, 1923). On every shoot 6–12 leaf-blades, which are 30–150 cm long and narrow lanceolate (Plate 26 A). Stems often compressed, with or without inflorescences; sometimes the stems are wanting. This plant is a modification of rather deep running water. In the Netherlands only found in the Zwarte Water near Genemuiden.

fo. **terrestris** Glück, Beih. Bot. Clb., 39, 313, 1923.

The leaf-blades are short or completely wanting. This modification has been found several times on the newly reclaimed soils in the Northeasternpolder.

2. **Scirpus lacustris** L. ssp. **flevensis** Bakker, nov. ssp. [1]

Differt a ssp. lacustre rhizomatibus sublentis, longitudine caulum vulgo minore, glumis nonnullis verrucosis, connectivis vulgo brevius pilosis, spiculis flores 2 et 3 stigmatibus praeditos gerentibus, achaeniis planioribus, in sectione transversa plano-convexis vel obscure triquetris. Differt a ssp. tabernaemontano rhizomatibus subduris, caulibus ad basin nunquam clavatis, glumis minus verrucosis, connectivis vulgo longius pilosis, spiculis flores 2 et 3 stigmatibus praeditos gerentibus, achaeniis nonnullis in sectione transversa obscure triquetris.

(Type: Herb. Bot. Dep. N.E. polder nr. 1153; 1952, Ketelveld, coastal area Yssellake).

The intermediate characteristics are further shown in a convincing way in the tables 1 and 2 and Plates 24 and 25. No varieties are distinguished, as the specimens are rather homogeneous.

This subspecies occurs in the shallow water of the coastal area of the Yssellake between the Ketel (the mouth of the Yssel) and the Ganzendiep.

In Genemuiden, the centre of rush manufacture in the Netherlands, the ssp. *flevensis* has been known as "fransje" for at least sixty years owing to its usefulness in the making of rush-bottomed chairs, for the stems are thin, uniform in thickness and tough. That is why this rush is regularly planted out in the coastal area between the Ketel and the Ganzendiep; so here these plants are propagated by means of the vegetative underground rhizomes.

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[1] The name "flevensis" has been derived from the Lake Flevo, which was situated in the area of the present Yssellake between 300 B.C. and 1200 A.D. This name has been proposed by Dr V. Westhoff.

As has been pointed out above, this rush has no hybrid nature, in spite of the intermediate characteristics. It will be explained below on what observations this conclusion is based.

In the first place, a comparative study has been made of the number of filled and unfilled fruits and pollen grains from the three subspecies involved. The relative number of good and bad fruits furnishes an indication of female fertility (Heiser, 1949). For this purpose thirty spikelets of each subspecies, grown on the coast of the Yssellake, were collected. The spikelets had been taken from the first stems of the rhizomes, as only stems and inflorescences of the same series should be compared (Seidel, 1952*a*). The average numbers per spikelet for filled and unfilled fruits in the ssp. *lacustris* as well as in the ssp. *flevensis* proved to be respectively 9 and 14; in the ssp. *glaucus* these numbers were 12 and 14. So in this connection the subspecies are well matched. Moreover, in table 2 it is shown that the total number of filled and unfilled fruits in the ssp. *flevensis* is about as great as in the other. Furthermore, in each of the subspecies about 94–98 % pollen grains proved to be filled and of a normal size, which shows the high male fertility.

TABLE 2

Some data on the fruits of the three subspecies of *S. lacustris* L. *sensu lat.*

Subspecies and locality	Average thousand-kernelweight in gr. (air dry)	From thousand fruits are (average):		
		unfilled	filled	
			trigonous	com-pressed
ssp. *glaucus*, Vollenhovense Meer . .	1.43	196	—	804
ssp. *glaucus* fo. *maior*, Biesbos . . .	1.81	182	14	804
ssp. *flevensis*, Ramsveld	1.85	213	394	393
ssp. *flevensis*, Ketelveld	1.85	158	443	399
ssp. *lacustris*, Ramsveld	2.65	119	876	5
ssp. *lacustris* var. *pendulus*, Ramsveld	2.82	181	816	3

Secondly, the germinative power of the ssp. *lacustris* proved to be nearly equal to the germinative power of the trigonous and compressed fruits of the ssp. *flevensis*; in the ssp. *glaucus* it reached a somewhat higher level. On the other hand, the ssp. *flevensis* was intermediate between the other subspecies as to the rapidity of germination (table 3). Before germination the fruits were kept in moist soil, at first six months at –2° C and after that six months at 2° C. The germinationtests were made between moist filter-paper in petri-dishes, which were placed in day-light.

Thirdly it appeared that the plants grown from the seeds of the ssp. *flevensis* were morphologically identical with the plants of the preceding generations, which does not occur in hybrids.

It does not call for further comment that these properties never

TABLE 3

Germinative power of the subspecies of *S. lacustris* L. *sensu lat.*

Subspecies	Average % germinated seeds after:				
	6 days	12 days	18 days	24 days	30 days
ssp. *glaucus*	0	85	90	91	91
ssp. *flevensis*					
a. trigonous fruits	0	44	63	76	78
b. compressed fruits	0	43	61	72	80
ssp. *lacustris*	0	7	62	78	82

are to be found together in hybrids or in the F 1 of crossings between lower taxa of the same species.

The diploid chromosome number proved to be 42 (counts made by Miss H. D. Schotsman), which is in accord with the number counted in the Scandinavian (Håkansson, 1928) and Dutch (Schotsman) material of the other subspecies. In Japanese specimens of the ssp. *lacustris*, Tanaka counted respectively 2 n = 38, 40 and 42. The first number refers to fertile plants, whereas the other were counted in variegated varieties with total or partial pollen sterility. As an examination of Japanese herbarium specimens has shown, it is not likely that the plants studied by Tanaka might lend themselves to a comparison with Dutch material.

Experience has proved that this subspecies cannot compete with the ssp. *lacustris*; at least for the present, as by the enclosure of the Zuydersea (now called Yssellake) the environment has been turned into permanent fresh water and the tidal effect has disappeared. If this rush had not been planted out regularly in consequence of its importance for the making of rush bottomed-chairs, it would probably have perished long ago. The fact that this subspecies only has been found between the Ketel and the Ganzendiep, where planting out occurred till recently, is in favour of this hypothesis. In accordance with this view the ssp. *flevensis* might be compared with the races of our cultivated plants, which cannot continue existence without the intervention of man.

The classification as a subspecies is an obvious fact. On account of the intermediate characteristics it is impossible to consider this plant as a variety of one of the other subspecies, whereas the classification as a separate species does not agree with the close affinity of the ssp. *lacustris* and *glaucus*, of which the ssp. *flevensis* is the intermediate. Nevertheless, as this rush grows in an environment where the ssp. *lacustris* reaches its optimal development, it is difficult to regard this plant as an ecotype. This does not exclude, however, the possibility that this subspecies may be adapted to an unknown habitat and it is open to question whether this habitat still occurs in this area. In this connection it is worth mentioning that after the environment in the Yssellake has turned into permanent fresh water, the ssp. *glaucus* has been almost crowded out by the ssp. *lacustris* in the coastal area between the Ketel and the Ganzendiep.

For three years I observed a transplant experiment with the three subspecies in a shallow and fresh pool near Blokzijl, where they grow without competition. As appears from this trial the ssp. *flevensis* does not seem to have the character of a modification, as the characteristics summarized in table 1, did not change at all.

Finally, it is still possible that the ssp. *flevensis* should be in fact a hybrid, which became apomictic. However, apomixis is not known of *S. lacustris*. As has been pointed out above, it is thought that the ssp. *flevensis* originated from crossing between the ssp. *lacustris* and *glaucus*, followed by back-crossings with the parents, which involved "introgressive hybridization".

The ssp. *flevensis* differs from the var. *β. bodamicus* Gaudin and b. *minor* Döll of *S. lacustris* by the round stems and the presence of about sixty percent flowers with 2 stigmas. In these varieties the stems are bluntly triangular above, whilst in the spikelets flowers with 2 stigmas have only sporadically been found. In the var. c. *trigonus* Döll on the contrary, nearly all the flowers have 2 stigmas. Probably these varieties are hybrids with *S. triqueter* L. (NEILREICH, 1859; LOUSLEY, 1931). Also *S. kalmussii* Ascherson, Abromeit et Graebner, as recorded from some parts of Germany, differs from the ssp. *flevensis* by the very thin, low and bluntly triangular stems above, the hypogynous bristles twice as long as the fruits and the nearly glabrous glumes, whilst all the flowers have 2 stigmas; in all probability this species belongs in fact also to *S. lacustris* L. *sensu lat.*

3. **Scirpus lacustris** L. ssp. **glaucus** (Smith) Hartman; Smith, Engl. Bot., 33, t. 2321, 1812; C. Hartman, Fl. Gev., 36, 1848; *S. tabernaemontani* Gmelin, Fl. Bad., 101–102, 1, 1805.

The ssp. *glaucus* is not always easy to distinguish from the ssp. *lacustris*, because several characteristics may overlap, as has already been pointed out above (table 1). Hence, the possibility does seem to exist that the highly fertile specimens with frayed leaf-sheaths, rather long leaf-blades, elongated spikelets, flowers with 3 stigmas scattered in the spikelets, glabrous or nearly glabrous glumes or long bearded connectiva at the tip are the result of crossings with the ssp. *lacustris* in one of the preceding generations. In the Herb. Bot. Dep. N.E. polder, for instance, specimens from Koedood, Oude Maas, are preserved with in each spikelet some flowers with 3 stigmas and a specimen from the Kamperisland with during flowering nearly glabrous glumes and at the tip rather long bearded connectiva. It must be kept in mind, however, that as a consequence of the plasticity the ssp. *glaucus* might vary according to the environmental conditions, e.g. the length and the diameter of the stems.

In the Netherlands the ssp. *glaucus* is a characteristic subspecies of the *Scirpetum maritimi* Tüxen, an association occurring sometimes in fresh but usually brackish water. According to IVERSEN (1936) this subspecies is "halophil", "oligo-mesohalob" and "polyhygroob", which means that it reaches its optimal development in a wet and brackish environment with a range of 0.1–10 $^0/_{00}$ Cl, which is the habitat of the *Scirpetum maritimi*. In this connection it must not be overlooked that in the tidal estuaries the chlorine concentration may increase to a much higher level during high floods. Although this subspecies is the ecotype of brackish habitats, it also grows, usually with a lower vitality and competition power, in a fresh environment. But I can fully agree with the statement of IVERSEN, as it might explain why the ssp. *glaucus* is only frequently recorded from the

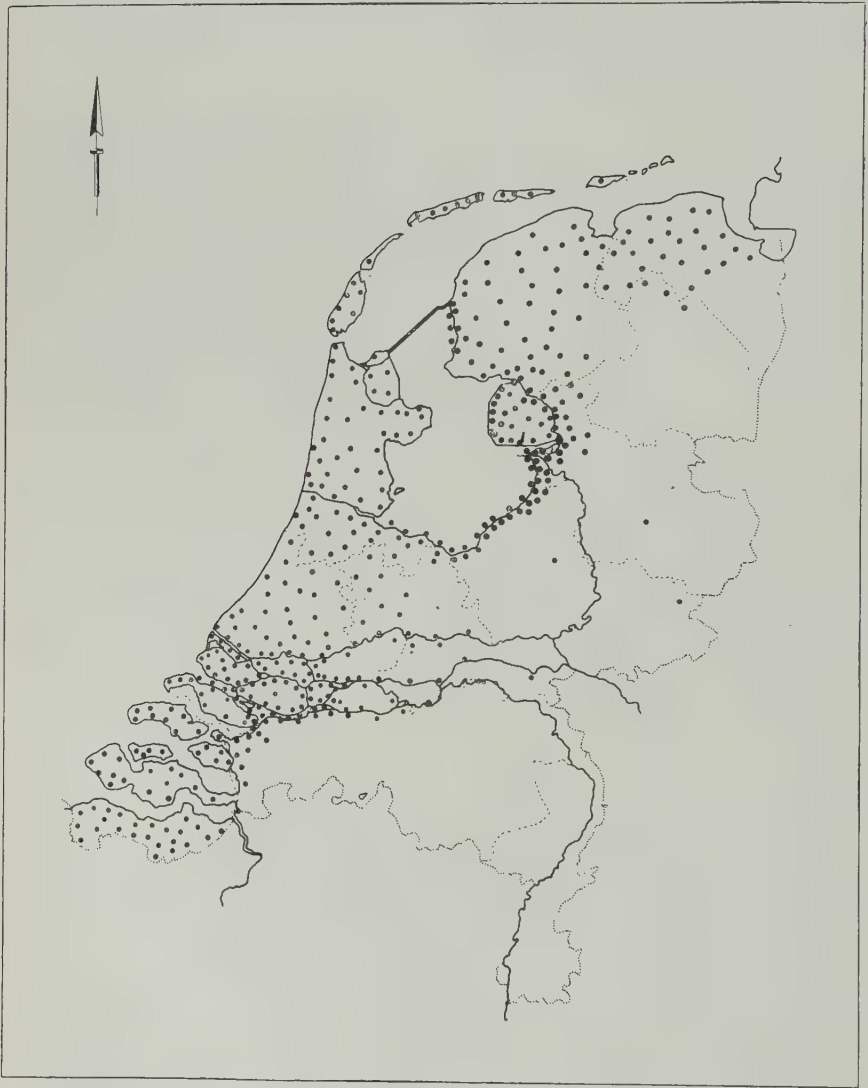


Fig. 2. Distribution of *Scirpus lacustris* L. ssp. *glaucus* (Smith) Hartman in the Netherlands. The data on this map are due to the herbaria mentioned in this paper, the "Nederlandsch Kruidkundig Archief" and the observations of the writer

Western part of the Netherlands, where the environment is often more or less brackish (Fig. 2).

With regard to the factor "water", this plant may be considered as a telmatophyte *sensu* IVERSEN, as it is able to grow in anaerobic and wet soils owing to the presence of aerenchymatic tissue. In contrast with the ssp. *lacustris*, this subspecies does not develop submersed "Bandblätter" (GLÜCK, 1923).

In the Netherlands the following variety and forms can be distinguished:

var. **compactus** Bakker, nov. nom.; var. *capitatus* Hausskn., Mitt. Geogr. Ges. Thür., 31, 6, 1888.

The inflorescences are capitate crowded (Plate 26). Seeing that on the same rhizomes stems with normal as well as with capitate inflorescences were observed, it is open to question whether this variety is of any systematical significance. It has been found in the Netherlands in the Kamperisland and Texel, and near Amsterdam, Blokzijl, Markelo, Rotterdam and Spakenburg.

fo. **maior** (Custor) Bakker, comb. nov., Gaud. Fl. Helv., 6, 337, 1830.

This form is characterized by the measurements of the stems and the inflorescences. The length of the stems is as much as 2.75 m and the diameter below 6 cm, whilst the inflorescences are large and strongly ramified (Plate 26). According to CUSTOR the colour of the stems is glaucous or green; the Dutch specimens, however, usually are glaucous, sometimes nearly green. But for the rest our specimens are in accordance with CUSTOR's description. LOUSLEY (1931), on the contrary, supposes that this plant should be considered as a hybrid between *lacustris* and *glaucus*. As a result of my observations the specimens in the Netherlands had better be called a modification, which comes into being when the ssp. *glaucus* grows as a pioneer in fresh, or slightly brackish, current water, rich in nutritive substances. In the Netherlands the fo. *maior* has only been found in the fresh or slightly brackish tidal estuaries in the S.W. and on the coast of the Yssellake.

fo. **tenuis** Bakker, nov. fo.

Caules tenues, ad basin diametro 3–6 mm.

(Type: Herb. Bot. Dep. N.E. polder nr. 1288; 1953, between Kampernieuwstad and Oosterwolde).

From ditches near the coast of the Yssellake and brackish and wet dune valleys specimens are recorded with low (40–80 cm) and thin stems (3–6 mm below), sometimes even faintly angular above. As appears from a transplant experiment those plants must be regarded as a modification owing to poor environmental conditions.

In gardens the var. *zebrinus* André from Japan with variegated stems is cultivated on a moderate scale. Only a profound study may prove if this variety in fact belongs to the ssp. *glaucus*.

THE HYBRIDS OF *S. lacustris* L. *sensu lat.* AND *S. triqueter* L. IN THE NETHERLANDS

The determination of these hybrids is by no means simple. Besides the usual lack of uniformity which one expects in a simple Mendelian cross the situation is, in all probability, greatly complicated by numerous back-crosses with the parents (LOUSLEY, 1931). It follows that the hybrid swarm of *S. lacustris* × *S. triqueter* will show a great variability, ranging from one parent to the other. In consequence, it is difficult to form a description which will fit all specimens. Moreover, it is sometimes impossible to decide whether the ssp. *lacustris* or the ssp. *glaucus* is one of the parents. Beside it, the fertility is often manifestly less than in the species, but rather fertile specimens may be found. In the Netherlands these hybrids are only recorded from the fresh tidal estuaries in the S.W., where *S. triqueter* occurs. The following hybrids are distinguished:

S. × carinatus Smith, Engl. Bot., 27, t. 1983, 1808 (pro sp.); *S.* × *duvalii* Hoppe, Sturm D. Fl., 1(9), 3(1), 1814 (pro sp.); *S. lacustri-triqueter* Neilreich, Fl. N. Oesterr., 126–127, 1859.

S. × *carinatus* was recognized as the hybrid of *S. lacustris* L. ssp. *lacustris* and *S. triqueter* by NEILREICH (1859). All the Dutch specimens I have seen may be classed under the var. *sub-lacustris* Lousley (1931). The description of this variety runs as follows: "Stem triangular above. Panicle large, exceeding the bract and resembling that of *lacustris*. Stigmas 2 or 3. Anthers bearded, in some plants. A tall stout plant". In this connection, it is worth mentioning that the plants described by SMITH and HOPPE have only 2 stigmas. In the following a short description of the Dutch material is given.

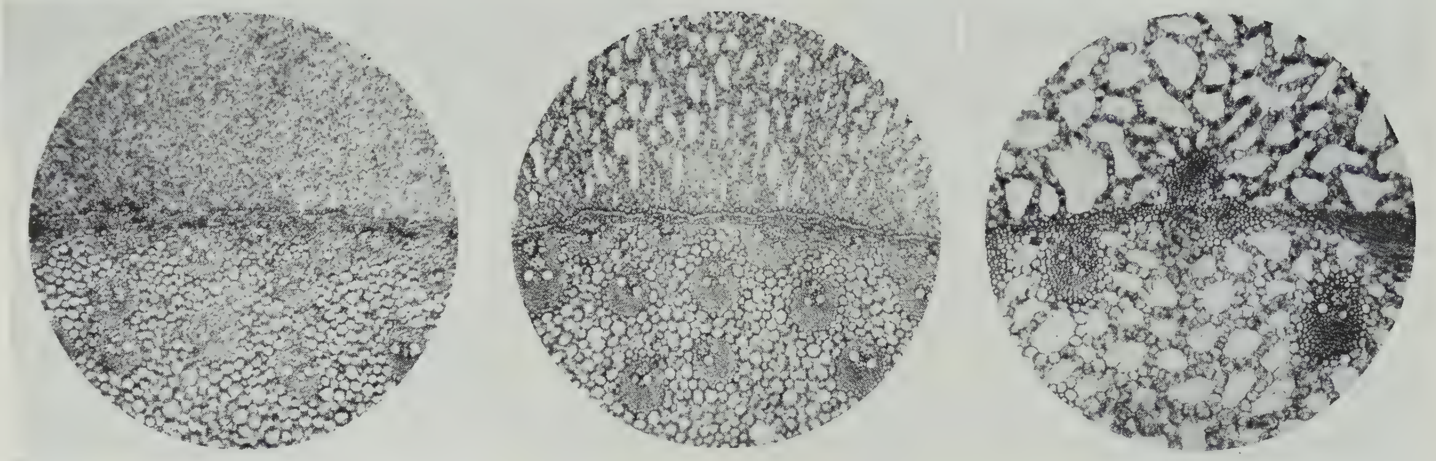
a. Herb. Bot. Dep. N.E. polder: near Malta in the Biesbos, about 1 m above mean low tide, with the putative parents, nr. 1353, leg. Bakker, Boer and Zonneveld, 1953.

In general habit, the hard, brittle and red-brown rhizomes, the round base, the fresh green colour and the length of the stems (as much as 2 m), on each stem the leaves with at least two distinct leaf-blades and the large panicles, mostly as long as or overtopping the lower bracts, it agrees with *S. lacustris* ssp. *lacustris*. It approaches to *S. triqueter* by the bluntly triangular upper part of the stems and the triangular and rigid lower bracts. With the exception of the midrib the glumes are glabrous. In every spikelet flowers with 2 and 3 stigmas occur (table 4). The connectiva are pointed at the tip, short bearded. Furthermore this plant is characterized by the production of about 90 % filled pollen grains and a small number of ripened fruits (about 5 %). These fruits are compressed, brown and able to germinate.

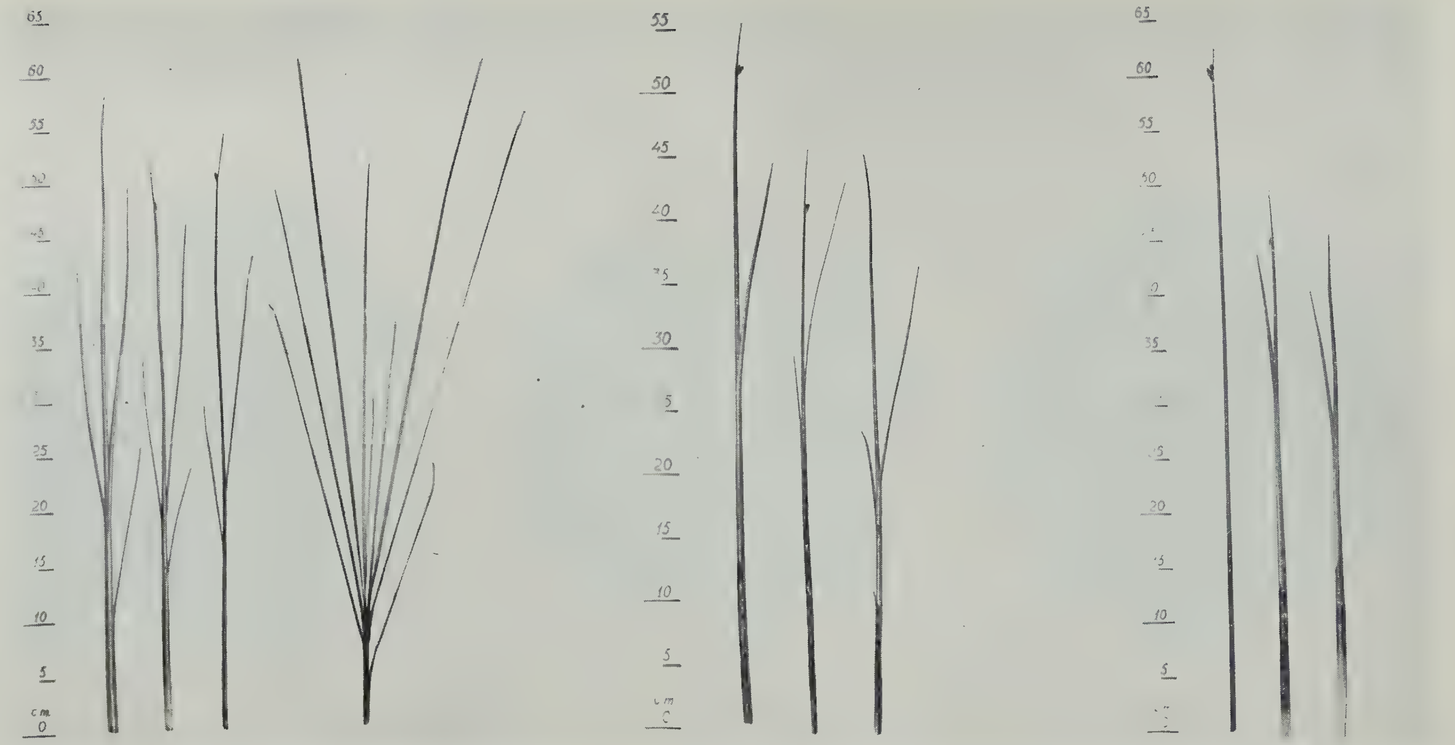
In 1952 I made a transplant experiment with this hybrid in a shallow and fresh pool near Blokzijl. As appears from this trial the characteristics summarized above did not change at all.

b. Rijksherbarium Leyden: Dordrecht along the Merwede, leg. Kloos, 1914; Dordrecht, Nieuwe Biesbospolder, leg. Kloos,

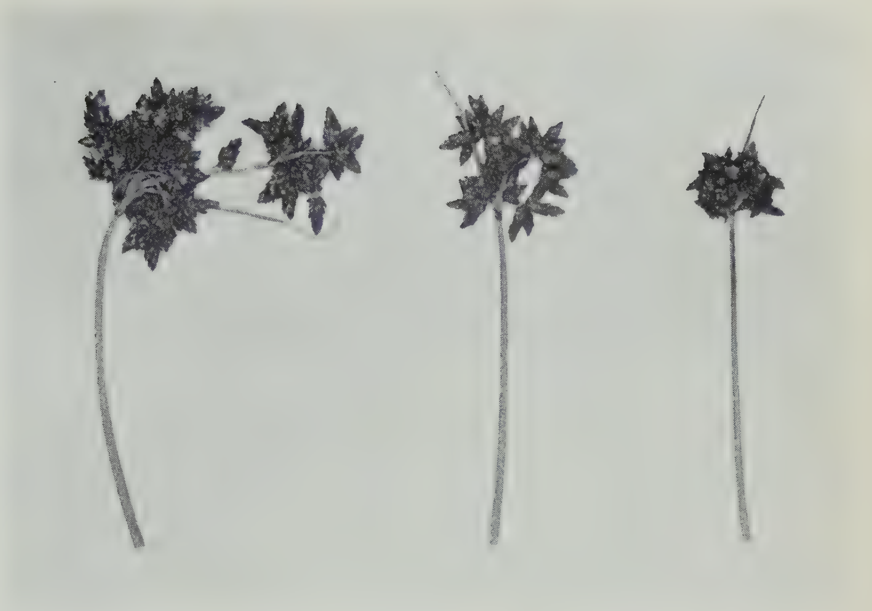
PLATE 24



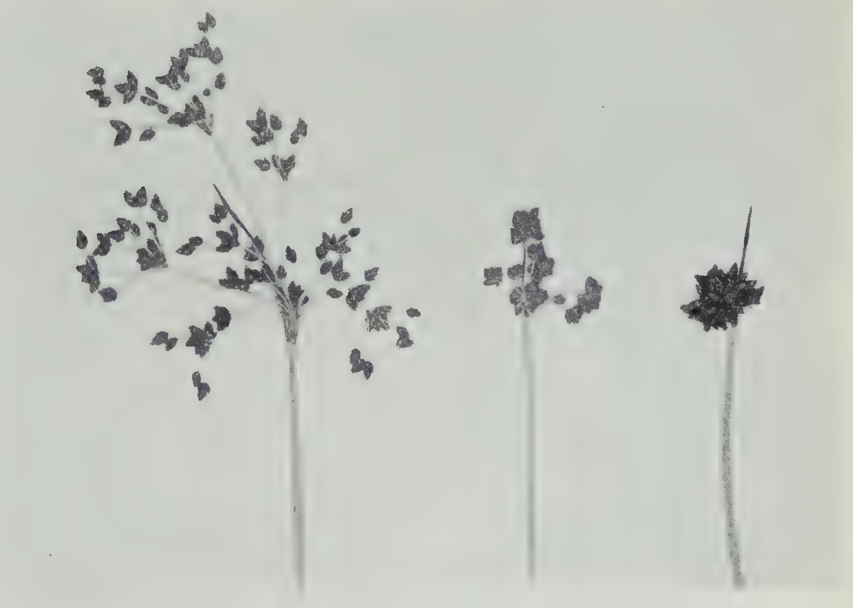
Cross sections in the corresponding rhizome-regions of the ssp. *lacustris* (left), *flevensis* (centre) and *glaucus* (right) of *Scirpus lacustris* L. *sensu lat.* (47 ×)



The growth of leaf-blades of *Scirpus lacustris* L. *sensu lat.* To the left the ssp. *lacustris* with 2-8 leaf-blades (the specimen with 8 leaf-blades belongs to the fo. *fluitans*), in the centre the ssp. *flevensis* with 1–2 leaf-blade(s) and to the right the ssp. *glaucus* with 1 leaf-blade or leaf-blades wanting



A Inflorescences of the var. *pendulus* (left), a normal specimen (centre) and the var. *capitatus* (right) of *Scirpus lacustris* L. ssp. *lacustris*



B Inflorescences of the fo. *maior* (left), a normal specimen (centre) and the var. *compactus* (right) of *Scirpus lacustris* L. ssp. *glaucus* (Smith) Hartman

Van Dijk and Prins, 1934 (Ned. Kruidk. Arch., 129, 45, 1935) and Rijswijk along the Maas, with the putative parents, leg. Kern and Reichgelt, 1943 and 1946.

In general habit, the length of the stems (as much as 2 m), the round base of the stems and the leaves with often two distinct leaf-blades on each stem, these specimens resemble *S. lacustris* ssp. *lacustris*. The material approaches to *S. triqueter* by the bluntly triangular upper part of the stems and the triangular lower bracts. The panicles are as long as or overtopped by the lower bracts. The spikelets are elongate and the glumes glabrous. In the spikelets nearly all the flowers have 3 stigmas, but in all the spikelets scattered flowers with 2 stigmas occur. The connectiva are short bearded. A rather large number of filled pollen grains has been counted. In all probability ripened fruits are formed, mostly trigonous.

c. Herb. Bot. Dep. N.E. polder: along the Oude Maas near Koedood, about 1 m above mean low tide, with the putative parents, nrs. 1767–1770, leg. Bakker and Boer, 1954.

In general habit, the red-brown rhizomes, the length of the stems (as much as 1.75 m) and the round base of the stems, it agrees with *S. lacustris* ssp. *lacustris*. It resembles *S. triqueter* by the rather weak and thin rhizomes (diameter about 0.5 cm), the weak stems, the bluntly triangular upper part of the stems, the colour of the stems, the leaves with not more than 1 leaf-blade on each stem and the panicles strongly overtopped by the triangular lower bracts. At one side the stems are often channelled for 5–20 cm below the panicles. With the exception of the midrib the glumes are glabrous. In each spikelet flowers with 2 and 3 stigmas occur (table 4). The connectiva are somewhat pointed at the tip, very short bearded. About 10–30 % filled pollen grains has been counted. Fruits are rarely ripened.

d. Herb. Bot. Dep. N.E. polder: on a coffer-dam in the Zuid-Maartensgat, Biesbos, about 1.50 m above mean low tide, with the putative parents, nrs. 1771–1772, leg. Bakker and Boer, 1954.

In general habit, the red-brown and rather hard rhizomes (diameter about 0.8 cm) and the fresh green colour and the length of the stems (as much as 1.75 m), it approaches to *S. lacustris* ssp. *lacustris*. It agrees with *S. triqueter* by the stems, distinctly triangular for a considerable distance below the panicles, the leaves with only one leaf-blade on each stem and the rather small panicles, strongly overtopped by the triangular lower bracts. With the exception of the midrib the glumes are glabrous. Mostly some flowers with 3 stigmas occur (table 4). The connectiva are pointed at the tip, scarcely bearded. About 40–50 % filled pollen grains has been counted. Some fruits are ripened.

By the stems, triangular for a considerable distance below the panicles, the scarcely bearded connectiva and the small panicles, this material approaches to the var. *sub-triqueter* Lousley. Owing to the length of the stems and the well developed reproductive organs I have still classed this hybrid under the var. *sub-lacustris*.

TABLE 4

Average and extreme numbers of flowers per spikelet with 2 and 3 stigmas in hybrids of *S. lacustris* L. *sensu lat.* and *S. triqueter* L.

Name and locality	2 stigmas	3 stigmas	Number of panicles studied
S. × *carinatus*, Malta	13(16–11)	4(7–2)	20
S. × *carinatus*, Oude Maas	8(11–4)	7(11–5)	15
S. × *carinatus*, Z. Maartensgat	15(19–10)	1(2–0)	18
S. × *scheuchzeri*, Jonge Deen	15(19–8)	2(4–0)	20
S. × *scheuchzeri*, Oude Maas	15(18–12)	3(7–1)	20

S. × **scheuchzeri** Brügger, Jahresber. Naturf. Ges. Graubünden, 108–111, 25, 1882; *S.* × *kukenthalianus* Junge, Mitt. Bot. Staatsinst. Hamburg, 73, 12, 1904; *S.* × *arunensis* Druce, Bot. Soc. Exch. Cl. Br., 68, 7, 1923.

The hybrid *S. lacustris* L. ssp. *glaucus* (Smith) Hartman × *S. triqueter* L. (*S.* × *scheuchzeri*) was for the first time described by BRÜGGER (1882). It is a curious fact, however, that BRÜGGER collected this hybrid in an area, where the putative parents did not occur. Moreover, it will be noticed that in BRÜGGER's description there is no reference to the male and female sterility.

Owing to BRÜGGER, JUNGE (1904) and LOUSLEY (1931) this hybrid has glaucous stems, bluntly triangular above, more or less asperous glumes and 2 stigmas. Furthermore an ill fruit formation is recorded by JUNGE. The Dutch specimens are usually characterized by dark- or grey-green stems, bluntly triangular above, more or less asperous glumes and often in the spikelets scattered flowers with 3 stigmas. The fertility is usually manifestly less than in the species. With regard to the scattered flowers with 3 stigmas it must be kept in mind, that in the ssp. *glaucus* scattered flowers with 3 stigmas are rather much found. In the following a short description of the Dutch material is given.

Herb. Bot. Dep. N.E. polder: Boerenplaat, nrs. 1351 and 1373, N. Jonge Deen, nr. 1353, and Rode Vaart, nrs. 74–75, in the Biesbos and along the Oude Maas near Koedood, nrs. 1774–1775, about 60–80 cm below mean low tide, with the putative parents, leg. Bakker and Boer, 1953 and 1954.

The rhizomes are thin (diameter 4–5 mm), weak, tough and yellow-white. The stems are weak, grey-green, bluntly triangular above and sometimes compressed or channelled for some distance below the panicles. The length of the stems is as much as 1.50 m, they have nearly all not more than 1 leaf with a distinct leaf-blade. The lower bracts are triangular and of different length, in the specimens of the Biesbos as long as or overtopped by the panicles. The glumes are more or less asperous, dull red-brown. Flowers with 2 stigmas predominate (table 4). The connectiva are slightly bearded or not at all. Many empty pollen grains are formed. A rather large number of fruits is ripened; the fruits are compressed and yellow-brown. This hybrid flowers in August.

In so far as may be judged of the herbarium material, the following specimens also belong to this hybrid:

Rijksherbarium Leyden: Dordrecht along the Maas, leg. Van Hoven; Rotterdam along the Nieuwe Maas, nrs. 2195–2196, leg. Danser and nrs. 4737–4742, leg. Jansen and Wachter, 1908 (in Prodr. Fl. Bat. ed. alt. as *S. lacustris* × *triquetrus* and in Fl. Bat. as *S. duvalii*; JANSEN and WACHTER, 1917); Rotterdam near the Schaardijk, leg. Danser, 1909; fore-lands along the Nieuwe Maas near Vlaardingen, nrs. 22616–22619, leg. Jansen and Wachter, 1918; Schiedam near the Sterrebos, leg. Kern, 1938; Rozenburg, leg. Vervoort and De Bruyn, 1944.

In each spikelet of rushes, collected on the fore-lands along the Nieuwe Maas near Vlaardingen in 1917 by Jansen and Wachter (nrs. 14923–14934), flowers with 2 and 3 stigmas occur in a ratio of about 5 to 2, whilst the outer glumes are asperous to some extent. The thin stems are bluntly triangular for a considerable distance below the panicles. The production of many empty and misshapen pollen grains and the bluntly triangular stems suggest, that this homogeneous material, in contrast with the ssp. *flevensis*, should be considered as a hybrid with *S. triqueter* L. In spite of the large number of flowers with 3 stigmas I consider this hybrid on account of the general habit and the asperous glumes as *S.* × *scheuchzeri* (JANSEN and WACHTER, 1917).

S. × *schmidtianus* Junge (*S. lacustris* L. ssp. *lacustris* × *S. americanus* Pers.), which is almost or completely sterile, has not been recorded in the Netherlands.

SUMMARY

In literature quite different opinions have been developed with regard to the species-concept of *S. lacustris* L. and *S. tabernaemontani* Gmel. In the nineteenth century several authors considered these species as modifications of *S. lacustris* L., owing to the resemblance, the unstable characteristics, the merging into one another under the influence of changing environmental conditions or the occurrence of intermediates. This does not exclude, however, the possibility that the unstable characteristics, the occurrence of intermediates and probably even the merging into one another should be ascribed to the growth of hybrids between the species mentioned above; from one locality this hybrid is on record. Consequently, in the twentieth century they are usually considered as separate species.

An examination of the specimens occurring in the Netherlands showed, that in one locality in our country a highly fertile intermediate grows, with the same chromosome number as the other two forms, whilst the plants developing from the seeds of the intermediate are equal in morphological characteristics to those of the preceding generations. It follows that on no account the intermediate can be a hybrid. It is thought that the intermediate has been originated by

"introgressive hybridization" *sensu* ANDERSON and HUBRICHT (1938), which means in this case by crossing of *S. lacustris* L. and *S. tabernaemontani* Gmel. followed by back-crossings with the parents. Moreover, in some instances the possibility does seem to exist that between these species cross-breeds with undiminished fertility are yielded. It follows that in some localities in the Netherlands the boundaries between these species have been obliterated. According to these data the above-mentioned species are considered to belong to the same commiscuum *sensu* DANSER (1950). On the strength of the fertility of the cross-breeds, the occurrence of gradation, the same chromosome numbers, the morphological resemblance and the fact that they reach their optimal development in different habitats, they are in this paper unitied into the same species. This means they are ecotypes (subspecies), respectively the ssp. *lacustris* and the ssp. *glaucus* (Smith) Hartman, of the ecospecies *S. lacustris* L. *sensu lat.* The intermediate has been described as the ssp. *flevensis* of *S. lacustris* L. *sensu lat.*, which, in all probability, continues existence in the habitat of the ssp. *lacustris* as a consequence of the planting out by man.

In the course of this examination data on the polymorphy, the distribution and the hybrids of *S. lacustris* L. *sensu lat.* × *S. triqueter* L. in the Netherlands have been obtained.

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NOTES ON RANUNCULUS FICARIA L. IN THE NETHERLANDS

I. INTRODUCTION. — REDUCTIONAL TRENDS AS A POSSIBLE INTERPRETATION OF FLOWER TYPES

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(Received Sept. 20th, 1954)

One of the most striking features in *Ranunculus ficaria* is its way of reproduction, which is mainly vegetative and which is usually achieved by means of the well-known tubercles born in the axils of the leaves. Though the production of good or apparently good fruits and seeds is rather rare, a number of swollen achenes may be observed yet. However, we do not find seedlings too often, notwithstanding their being easily recognizable by the one single fanshaped cotyledon they possess. These facts have led to many investigations in the field of general biology, anatomy (seeds, tubercles, cotyledon), physiology, morphogenesis etc.

Flower structure and its variation and also diversity in vegetative parts (leaves) have been studied along taxonomic and phytogeographical lines; several botanists have conceived the lesser celandine as belonging to a separate genus, viz. *Ficaria.*[1]

The area of distribution of the species or species-complex occupies the whole of Europe and adjacent regions of Asia and Africa.

Our knowledge of this plant has also been extended by field studies and cytological investigations and by crossing experiments.

H. Winkler and co-workers published a series of papers under the title "Bausteine zu einer Monographie von Ficaria" in Beitr. z. Biol. d. Pflanzen in the years 1924–1933. Volume 21 (1933) procures a copious list of previous literature, which need not be repeated here.

The finding of a type of *Ranunculus ficaria* with aberrant flowers and new to the Netherlands led us to another investigation of this well-known plant along various lines. It was considered to be of importance to study the new type, already known from Italy (Delpino 1897), Austria (Berg 1899) and probably from England (Marsden-Jones 1935), and also to establish whether data, obtained in the Netherlands, tally with those from other parts of Europe.

Ranunculus ficaria is a polymorphic species. In the introduction we mentioned already variation in characters of leaves and flowers. The flowers vary in number and shape of flower parts and also in size. Variation in number will not be treated here.

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[1] In the present article we follow the nomenclature of the Dutch flora works.

When studying populations in a certain and more or less restricted area, one gains a notion of the common width of variation,[1] so that divergent types can be discerned with ease.

In the Netherlands we find the bright yellow flowers of this species to be different in size within certain limits. Hence, some specimens with very small aberrant flowers and with badly developed stamens, occurring in the field together with the normal type, were rather striking.

The "normal" plants and the aberrant type, which will provisionally be called *micrantha*, were found in the Netherlands for the first time in the province of Groningen in a mixed population at the edge of a wood on the slope of a little ditch facing south. Later on we found *micrantha*-plants and specimens with transitional flower types in several other places in nature in the north of the Netherlands and in the botanic garden ,,De Wolf" in the village of Haren (near the town of Groningen). From herbarium studies and oral information, however, we got the impression that *micrantha* is not (yet) known in other parts of the country.

The original area did not occupy more than ca 20 square metres and apparently was uniform with regard to ecological conditions. There were but few *micrantha* specimens and they were scattered between the normal plants. No real differences in vegetative characters could be traced yet; perhaps in *micrantha* the plants and their leaves also are somewhat smaller in size than is the case in the normal type; tubercles are abundant in both of them. In some chromosome countings in roottips we found the somatic chromosome number to be $2n = (\pm)\ 32$, thus both types are (auto) tetraploids as is *Ranunculus ficaria* in the greater part of its area of distribution. A diploid and more or less fertile type, known from Great Britain (cf. MARSDEN-JONES 1935), Portugal (BARROS NEVES 1942), Sardinia (NEGODI 1930) and maybe from France (CLOS 1852) has $2n = 16$; in some places also the occurrence of triploids, pentaploids and hexaploids has been established.

Apart from variations the flower in *Ranunculus ficaria* usually is composed of 3 "sepals", 8 "petals" and a great number of stamens and pistils.

The petals of the normal type, as far as seen and measured by us, vary in length from 6–15.5 mm and in width from 2.5–6.8 mm. Also the petals of one flower show differences between them. The average length is 10.8 mm, the average width 4.4 mm, based on measuring of 131 petals and on frequencies in value classes of 1 mm each. Greater length of petals is not always correlated with greater width, so that the petals also may vary in shape. The petal indices, being length over width, are between 1.6 and 3.5 (once 4.5?); the average value for petal index is 2.6 (172 petals).

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[1] In this paper the term variation is used in its widest sense, denoting any kind of diversity irrespective the causes.

The figures found in *micrantha* are different from those in the normal type. We did not undertake statistical work, but at any rate the differences are so conspicuous that they can be used as a discerning character even in the field.

Length of petals in *micrantha* (102 petals measured) was 5.0–8.0 mm, average 7.1 mm; width of petals 1.8–3.8 mm, average 2.5 mm. The petal index of *micrantha* is obviously greater than in the normal type, viz. 2.1–4.3, average 3.0 (132 petals). Thus these petals not only are smaller in size but also relatively narrower and the flowers are strikingly different from the smaller flowers of the normal type.

On further observation we found that the small *micrantha*-flowers had badly developed stamens or even no stamens at all. In the first case these stamens were not more than thin and whitish threadlike organs with highly underdeveloped pollen or without any pollen. The flowers, instead of being hermaphrodite, have become functionally female by reduction of the androeceum.

Differences in the expression of sex as well as self-sterility and apomixis to a certain degree are known from various species of the genus *Ranunculus* (MARSDEN–JONES and TURRILL 1929, 1935).

As the reduction of the androeceum might be conceived as a barrier to the ineffective selfpollination at least and thus might mean a certain adaptation to crosspollination, a study of the relations between flower types and pollinating insects became necessary.

The chief pollinating insects on *Ranunculus ficaria* were species of *Meligethes* (Coleoptera), *Apis mellifica* (Hymenoptera) and *Scatophaga stercoraria* (Diptera). Species of *Bombus*, *Formica*, *Tubifera* and butterflies as pollinators were scarce; I observed *Vanessa urticae* as a visitor once or twice. (cf. MARSDEN–JONES 1937).

In the normal flowers the insects find pollen and nectar, nectar being secreted in small scales at the base of the petals. Even those insects that search for nectar only, get covered with pollen from the extrorse outer stamens unintendedly. Female *micrantha* flowers also excrete nectar, as can be concluded from the presence of glittering drops in the little scales on the base of the petals and from the behaviour of the visiting insects.

With regard to pollen transport on a longer distance *Apis* and *Scatophaga* will be most effective; *Meligethes* are much less mobile and thus less useful as pollinators. For they will often bring about pollination between neighbouring members of one clone only, which will be as ineffective as selfpollination in the selfsterile *Ranunculus ficaria*.

From the type of flower no windpollination could be expected. Indeed no pollen was "caught" on a sticky plate, placed vertically in the field near to a population of *Ranunculus ficaria*.[1]

In the light of entomophily MARSDEN–JONES (1935) explained his observations that seed development is better in sun plants than in shade plants. This also implies a great dependence upon the type of weather, in particular while *Ranunculus ficaria* flowers so early in spring.

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[1] Experiments by mr J. M. Bonga and mr L. M. Schoonhoven.

For the purpose of investigating the possible biological sense of the little female flowers of the *micrantha* type we made a comparitive study of insect visits both to the normal and the *micrantha* type. For these pollination studies it was necessary to select comparable habitats, which could easily be done because of the occurence of the two types in mixed populations.

We studied insect visits to *Ranunculus ficaria* in such a mixed and limited population first on a sunny slope of a ditch facing south. On mere observation we noticed that bees, going from one plant to the other, passed over the female specimens without even touching them or paying any attention to them. This statement could be made repeatedly. Only the little black flower beetles of the genus *Meligethes* are to be seen rather often in the female flowers; as has been explained above, however, they may be little effective in crosspollination.

Countings were made to establish these differences in number of insect visits to both flower types more exactly. For that purpose we selected a little patch of ca ½–1 square metre in a mixed population, so that we were able to keep an eye on all the flowers. Results are listed in the following table:

Nr.	Insects	Nr of flowers		Nr of visits		"Inspection" Micrantha	Duration of observ.
		Norm.	Micr.	Norm.	Micr.		
1	Hymenoptera . . .	>	<	14	1	2	40 min.
2	Hymenoptera . . .	15	9	35	4	3?	75 ,,
	Diptera	15	9	23	1	—	75 ,,
	Coleoptera	15	9	4	—	—	75 ,,
3	Hymenoptera . . .	25	9	10	1	—	45 ,,
	Diptera	25	9	16	4	—	45 ,,
	Coleoptera	25	9	3	—	—	45 ,,
4	Hymenoptera . . .	12	7	7	3?–0	1(–4?)	60 ,,
	Diptera	12	7	11	1	—	60 ,,
	Coleoptera	12	7	1	5	—	60 ,,

In this table the term "inspection" indicates that the insects, when investigating the *micrantha*-flowers, either alight cursorily and without working or keep at a little distance.

The experimental area has always been chosen after careful introductory observation to ascertain that it was abundantly visited by insects. But the great abundance of normal flowers as compared with those of the *micrantha* type might have influenced the differentiation in the number of visits (cf. PERCIVAL 1947). For that reason we started another series of countings in the spring of 1954 in which we used two comparable small areas with ca equal numbers of normal and *micrantha* flowers respectively, close to each other and somewhat distant from the remaining populations. However, results of one counting only can be given because the weather was too bad and flying insects too scanty to procure sufficient figures and more reliable data. It is hoped that inquiries of this kind can be continued.

In the first examination 11 normal and 9 *micrantha* flowers were involved. Time of observation 75 minutes. The results are presented in the following table:

Insects	Normal flowers	Micrantha
Hymenoptera (mostly A is mellifica) .	18	3
Diptera	15	1
Coleoptera	3	0

The figures in the tables speak for themselves. They might have been even more evident had we counted the visits to every flower separately, instead of every visit as a whole. For the bees in particular visit several normal flowers in one flight, whereas in the case of *micrantha* they usually get through one single flower only.

Thus with regard to chances of pollination the facts are against *micrantha*. And as we hardly could yield any seeds judged to be more or less viable from a *micrantha* plant even after abundant artificial crosspollination with the normal type and never succeeded in raising progeny yet, we must conclude that in the case of *micrantha* reproduction is exclusively vegetative or very nearly so.

We cannot give details yet concerning the causes of unattractiveness of the *micrantha* flowers to insects. We mentioned the differences in number of the two types of plants. Moreover some properties at least are obvious in this respect, viz. the smallness and the sometimes slightly dull yellow colour of the flowers and the absence of stamens or functional stamens in *micrantha*.

In experiments with the normal type of *Ranunculus ficaria* we already gained some evidence that flowers without petals and also those from which the stamens had been taken away are less attractive than complete flowers. This holds true, as far as we can see now, particularly for bees. On the other hand it seems possible to stimulate insects, and again particularly bees, to visit *micrantha* by placing a cluster of normal stamens in the flowers. More experiments along these lines are desirable.

In conclusion we may state that the *micrantha* type of flower in *Ranunculus ficaria* prevents the ineffective selfpollination, it is true, but it cannot be considered as an adaptiveness to crosspollination, because it is hardly visited by mobile pollinating insects.

DISCUSSION

It is known from various plant species that apomixis goes together with selfsterility and with polyploidy (GUSTAFSSON 1946–'47; STEBBINS 1950).

Ranunculus ficaria is mainly known as an apomictic species. Its vegetative reproduction by means of axillary tubercles may be combined with a very poor development of but few seeds. Seed-formation may be achieved by agamospermy, but mostly is the result of crossfertilization, though the pollen is partly unviable (METCALFE 1939; BARROS NEVES 1942). The plants are highly selfsterile. Production of seeds, however, is not only checked by selfsterility, but it is also opposed by the presence of the axillary tubercles and probably by material influences of other vegetative parts (PERJE 1952). Development of the embryo is often disturbed in an early stage (METCALFE 1939).

Although there are some indications that in *Ranunculus ficaria* var. *ficaria* the result of the process of sexual reproduction in some degree depends on external conditions, it generally is very inconsiderable. The few apparently good seeds produce still fewer seedlings, which are liable to any kind of damage. (These facts hold for the tetraploid *Ranunculus ficaria* var. *ficaria;* the diploid fertile type, named var. *fertilis* Clapham (CLAPHAM, TUTIN and WARBURG 1952), will be left out of consideration here).

In the light of the present information we might consider the flower of *Ranunculus ficaria* as a rather functionless organ, the characters of which will have a low selective value in extensive parts of the area of distribution of the var. *ficaria.* Whether the flower is to be considered even as harmful and thus as being of negative selective value, will depend on the establishment of unfavourable influences of the flower on tubercle production.

With an organ which is practically functionless there is a good chance of survival for a series of its variants, which will hardly be subject to eradication by selection. By this also reductional types may continue to exist. And in tetraploid *Ranunculus ficaria*, under consideration here, even flowers with reductional trends in which the sexual organs are involved can maintain themselves, because in this plant such reductional processes are supported by ample vegetative reproduction.

As to the possible biological sense of the little female flowers of the *micrantha* type we might suggest that these flowers could be conceived as representing an advanced stage in a reduction process involving the flower of tetraploid *Ranunculus ficaria.* The existence of transitional types seems to confirm this idea. A similar process possibly leads to a type with male flowers by reduction of the pistils. However, no such completely male flowers have been seen by us, but they are known from Great Britain (MARSDEN-JONES 1935).

An other seemingly good interpretation—furtherance of cross-pollination—proved to be intenable in fact. The combined reduction in two different ways, leading to the occurrence of both male and female flowers and thus to dioecism might be conceived not only as a mere reduction but, on the other hand, as an improvement of the present situation. For it might also mean an escape from asexuality by exclusion of the ineffective selfing and by making crosspollination and crossfertilization the only possible cause of sexual reproduction. This mechanism, however, as has been explained above in the case of the female flower, does not work because of lack of attractiveness to insects; it could function only when accompanied by the development of a type of insects adapted to those unisexual flowers. And even then success might be doubtful, because it is known that it is not only lack of sufficient crosspollination which prevents the production of viable seeds in the tetraploid; there are also factors inherent to the ovules themselves, disturbing their further development (Metcalfe 1939; Perje 1952), and to the pollen.

Although the tetraploid spreads abundantly by means of its tubercles its asexuality is detrimental in so far that it reduces variability. Thus sexual seed development would be important yet, for it is a process producing a quantity of different types from which selection makes a choice and which consequently may become particularly valuable when the species moves to new habitats or when ecological conditions change in an area already occupied by the species.

In the present stage of affairs the adaptive capacity will be low. On account of this fact and of the flower reduction one might consider the tetraploid *Ranunculus ficaria* var. *ficaria* even as a biotype being on its way to extinction.

It seems worth while at any rate to pay attention to flower development and flower reduction in *Ranunculus ficaria*, both in its diploid and tetraploid type and to see whether this species corroborates Darlington's statement (1939): "apomixis is an escape from sterility, but it is an escape into a blind alley of evolution".

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A CASE OF ABNORMAL FLOWER STRUCTURES CONNECTED WITH REDUCED FERTILITY IN SOLIDAGO VIRGAUREA L.

BY

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With plates 27 and 28

(*Received Sept. 30th, 1954*)

In 1949 the author noticed *S. virgaurea* with the spreading part of the ray flowers, the so called rays, "split" into narrow lobes (Plate 27 B; a normal individual is illustrated in Plate 27 A). The observation was first made on a plant, that had settled with some normal ones into a flower box; it seems probable that the plants have been brought there as "seeds" among the soil rests from a cleaned collecting container. Having thus become acquainted with the modified plant, similar individuals could be collected in nature; (Baarn, province of Utrecht; on the slopes along a railway, September 1949, specimens in herb. pr.).

An examination of the abnormal flower structures provides the distinction of two groups, as a result of the floral organization of *S. virgaurea*, there being two types of flowers in the head: the outer zygomorphic, female ray flowers and the inner actinomorphic, perfect disk flowers.

The flower differences observed may be characterized as follows.

The differing ray flowers show from one to five narrow lobes of varying breadth. Some instances are represented in Fig. 1, B, C, D and E.

The differing disk flowers show deviations in corolla structure. The anthers are free in most cases and no more united; occasionally a few were found to be united. Some instances are illustrated in Fig. 2, B, C, D and E. Pollen production is reduced or wanting.

Drawings are given both of a normal ray and a normal disk flower and of some main forms of abnormal ones. The description hereafter relates to the altered flower parts and to the pollen production only.

NORMAL FLOWERING HABIT

Ray flower (Fig. 3, A). One side of the corolla is extended into a single, broad, flat, spreading lobe, in form and size typical of the species (this part is named in Floras in plural: rays, the term that is used above). Pappus hairs ± equal in length.

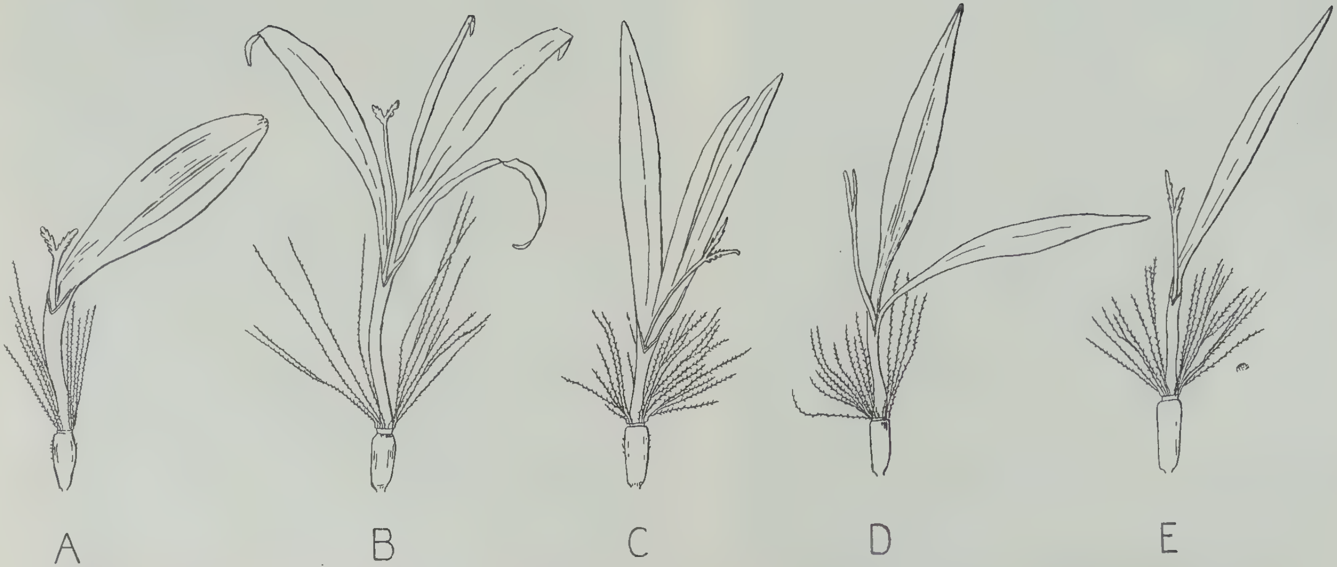


Fig. 1. *Solidago virgaurea* L. A, normal ray flower; B, C, D and E, differing ray flowers; pappus omitted partly to show corolla. 7 ×

Disk flower (Fig. 2, A). The corolla is expanded at the top into 5 equal lobes. The 5 anthers are united by their edges into a tube and produce pollen.

ABNORMAL FLOWER STRUCTURES

Ray flowers (Fig. 1, B, C and D). Development of 4, 3 and 2 narrow lobes of various breadth; the lobes are bent into different directions and in instances Fig. 3, B and C are more or less united. Pappus hairs often unequal in length.

Ray flower (Fig. 1, E). Development of one narrow lobe.

Disk flower (Fig. 2, B). Corolla abnormal by having a reduced number of lobes of deviating forms. There are ± 5 free anthers. Pollen little or wanting.

Disk flower (Fig. 2, C). Formation of a small, irregular, green, calyx-like structure; the tube above bears ± 5 petal-like anthers, which in some instances were found to produce pollen.

Disk flower (Fig. 2, D). There are ± 5 irregulary shaped corolla lobes, some of which were often noted to be united and all of them often coherent at the tip. There are 2–5 free anthers. Pollen is seldom produced.

Disk flower (Fig. 2, E). Formation of a sympetalous, cucullate structure. There are 2–5 free anthers. No pollen ascertained.

Transitional forms may be found.

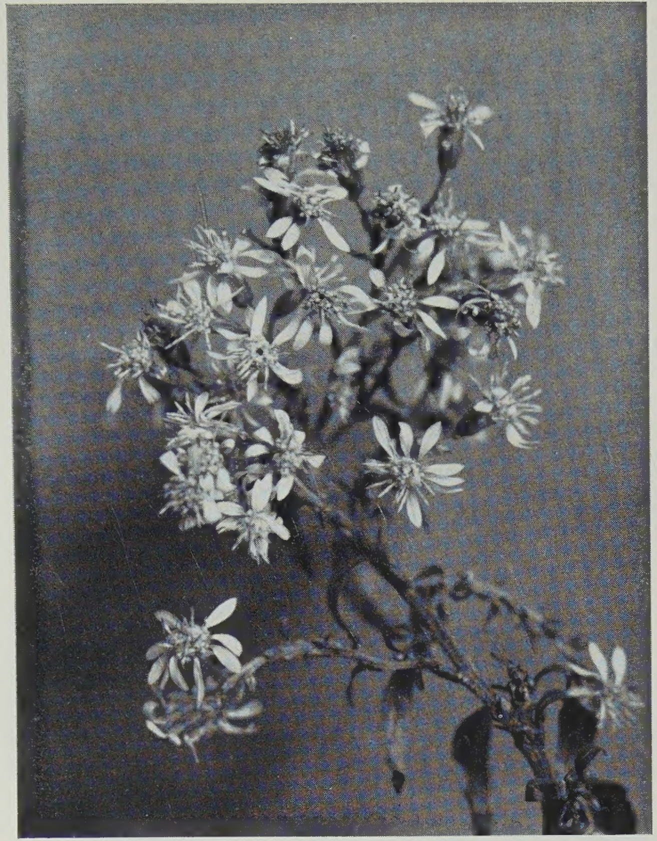
The normal heads include 8–12 ray flowers and 11–17 disk flowers. Approximately the same numbers were counted in the heads with abnormal flowers, so that there seems to be conformity in the composition of the flower-heads.

ROUY (ROUY, FOUCAUD et CAMUS, 1903, Flore de France, 8: 133–138) mentions of *S. virgaurea* a considerable number of forms and varieties included in these. In the description of these the variation stated of the outline of the foliage leaves is remarkable. The lower leaves of the varieties constituting the form I, *S. vulgaris* Lamk. are indicated from ovate and elliptical to lanceolate. In individuals with abnormal flowers, lanceolate leaves appear to predominate. This shape is conspicuous even in the radical leaves (Plate 28 A). The involucral bracts too are more slender than in the normal plant. It is emphasized that the leaves are not malformed or abnormal in color.

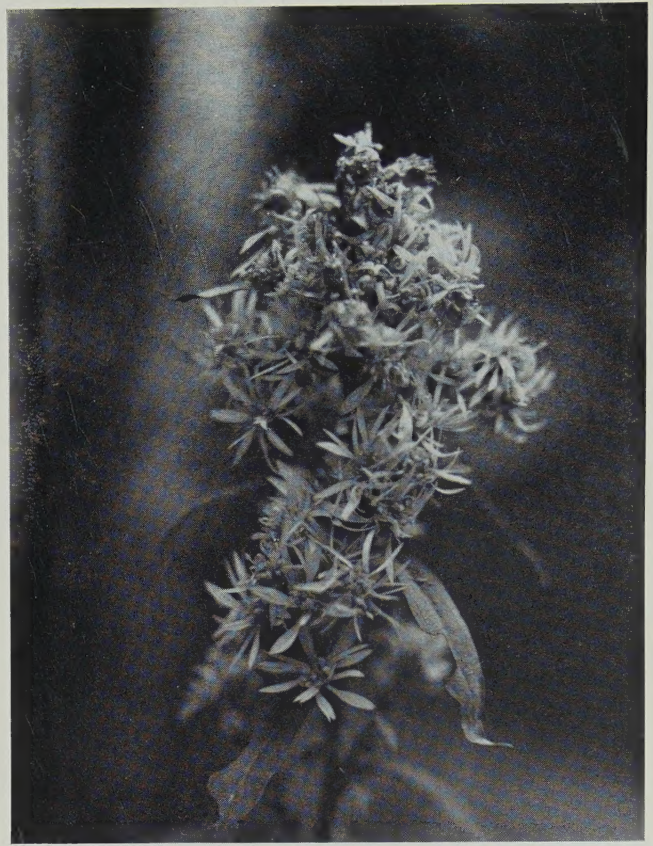
The differing individuals nevertheless develop fruits, although the number of achenes remains considerably below that produced by the ordinary plant. The normal *S. virgaurea* has relatively few abortive fruits in the heads. An average of ± 80 % sound achenes was found. The plants with differing flowers appeared to have a maximum of ± 50 % of the ovaries developed into fruits; however, in most cases the percentage is considerably lower.

It seems possible that the formation of achenes in the differing flowers is, at least for a part of the latter ones, a case of apomixis, because some heads were noted to contain mainly flowers without pollen grains on the stigmas, while the ovaries were apparently developing.

PLATE 27

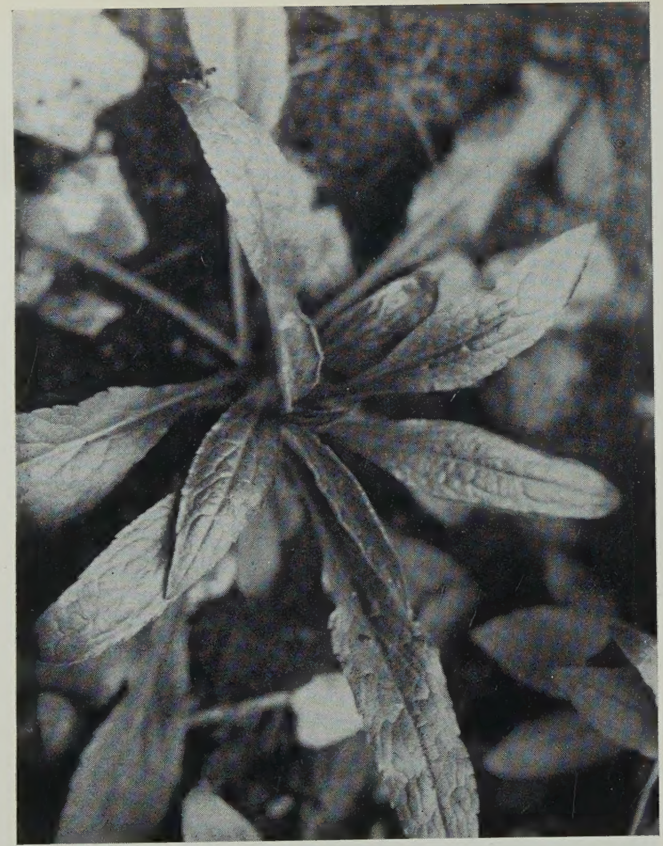


A *Solidago virgaurea* L. Normal plant

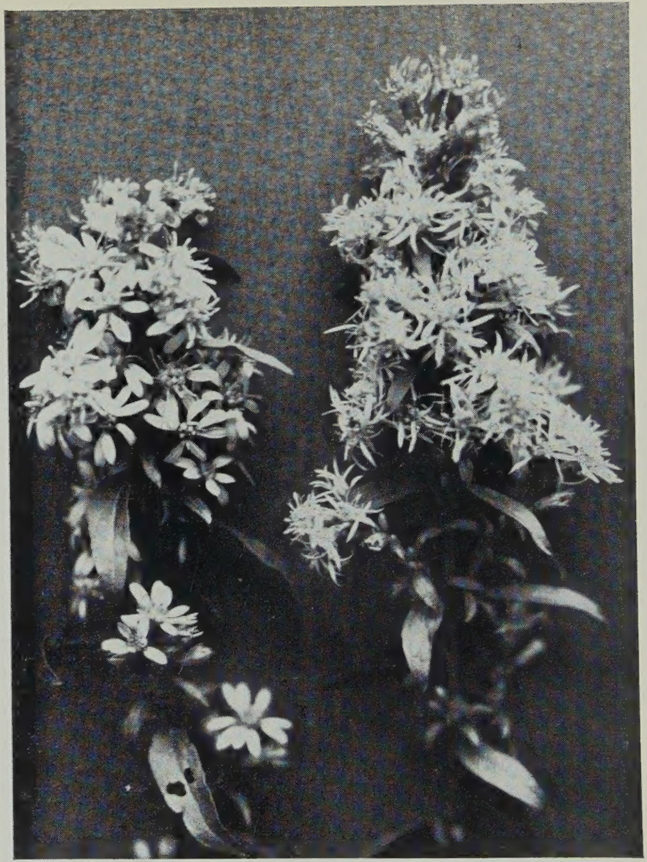


B *Solidago virgaurea* L. Individual with differing flowers

PLATE 28



A *Solidago virgaurea* L. Breeding experiment with abnormal plant. Radical leaves



B *Solidago virgaurea* L. Breeding experiment with abnormal plant. Stems with ordinary and differing flowers on the same rhizome

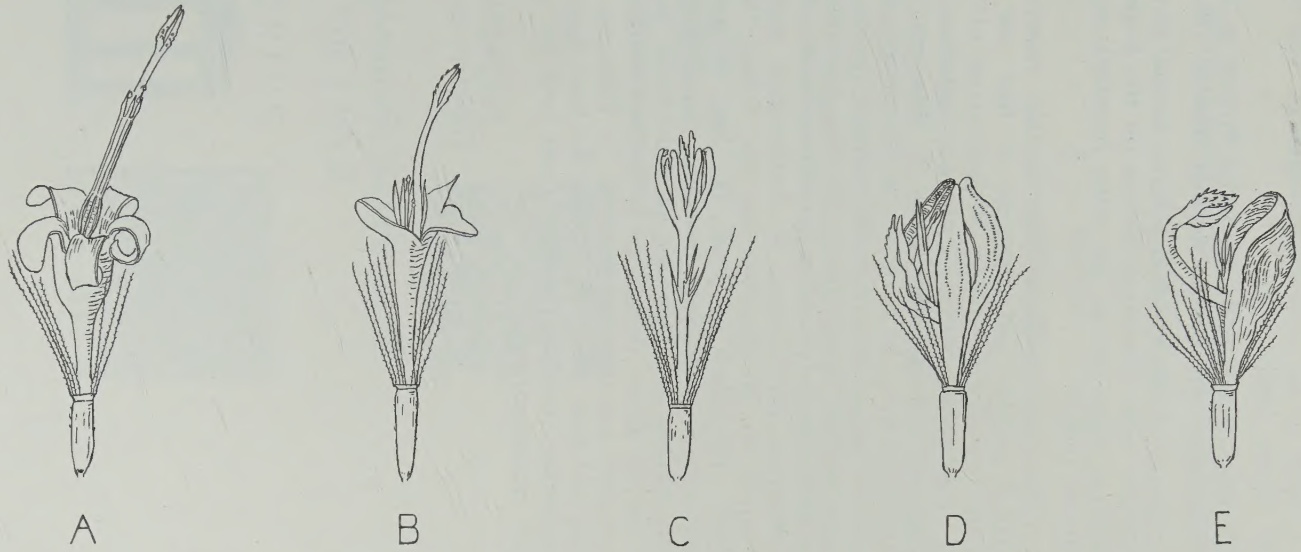


Fig. 2. *Solidago virgaurea* L. A, normal disk flower; B, C, D and E, differing disk flowers; pappus omitted partly to show corolla. 7 ×

In a breeding experiment, started 1951 with the abnormal plant first noticed, ± 50 % of the achenes germinated. The descendants appeared to be of two kinds, viz.:

a) the plant develops shoots with abnormal flowers as well as, on the same rhizome, stems having normal flowers (Plate 28 B);

b) the plant produces shoots which first form normal flowers at the top and continue with abnormal flowers on the lower branches and, in addition, there are on the same rootstock stems having ordinary flowers only.

The flower differences outlined bear certain resemblances to structures of floral cecidia and attempts to find out the cause responsible for the irregular behaviour of these plants of *S. virgaurea*, therefore, seem reasonable. Several external conditions were considered and studied. (To mention some. 1. Consumption of the foliage, sometimes resulting in bareness of the plants, possibly by birds; the occurrence appeared to coincide with the flower deviations. 2. An Aphid was noticed living among the abnormal florets in the heads; the same kind appeared to occur in ordinary heads of Goldenrod too, without affecting the flowers. 3. Individuals with differing flowers were noted to be attacked on the foliage by *Erysiphe cichoracearum* D.C.—identified by Prof. Dr Joh. Westerdijk. The latter hypothesis seemed promising; however, sound plants infected with the Powdery Mildew mentioned did not show flower disturbance). The causation of the flower deviations is not yet understood.

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